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BODY PROPORTIONS OF MAINLAND AND ISLAND LIZARDS

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INTRODUCTION

The original scope of the measurements presented in this paper was to provide evidence regarding the following questions: (1) Do island populations differ in their proportions from conspecific mainland populations? (2) If so, are these differences genetic or not? (3) Is the variation haphazard or are there parallel trends in island populations? (4) Are there any indications to suggest an adaptational value of the varying features?

This set of questions remained in the fore; however, in the course of my calculations changes of body shape were noted depending on growth and size, the appreciation of which exceeded the original scope. Owing to evidence common to both, and owing to cross relations in subject matter, the two viewpoints, island adaptation and allometric changes, cannot very well be separated so that they may find their place here side by side.

The species mainly under examination in this paper is *Lacerta serpa* Raf. = *L. sicula* Raf. The South Italian mainland lizards are representatives of the race *L. serpa typica* = *L. sicula sicula*, the North Italian ones belong to the more northerly race of *L. serpa* (= *sicula*) *campestris*. The paper presented here is in many respects a continuation of former publications (see Kramer, 1946; Kramer and Medem, 1940; Kramer and Mertens, 1938).

METHOD

The methods of measurement may be mainly inferred from Kramer and Medem, 1940; only the counting of the verticils of the tail have been added and will be described on p. 202.

The differences in proportion that form the object of our investigation are very small indeed. In most cases simple two class comparisons were not sufficient to secure them statistically. Advantage could be taken of the fact that the material in the majority of cases could be collated with an eye on more than one criterion. The statistical method to exploit such conditions is the Analysis of Variance.[1]

With one exception (Monacone) the proportions both of mature and newly hatched individuals were examined. The latter were bred in my cultures at Naples.

The trouble entailed by dealing with such slight differences might be avoided by choosing populations of islands of an older geological age. In that case, how-

[1] Cf. Snedecor. Acknowledgments are due to Dr. A. Bückmann and Prof. W. Ludwig for advice on matters of statistics.

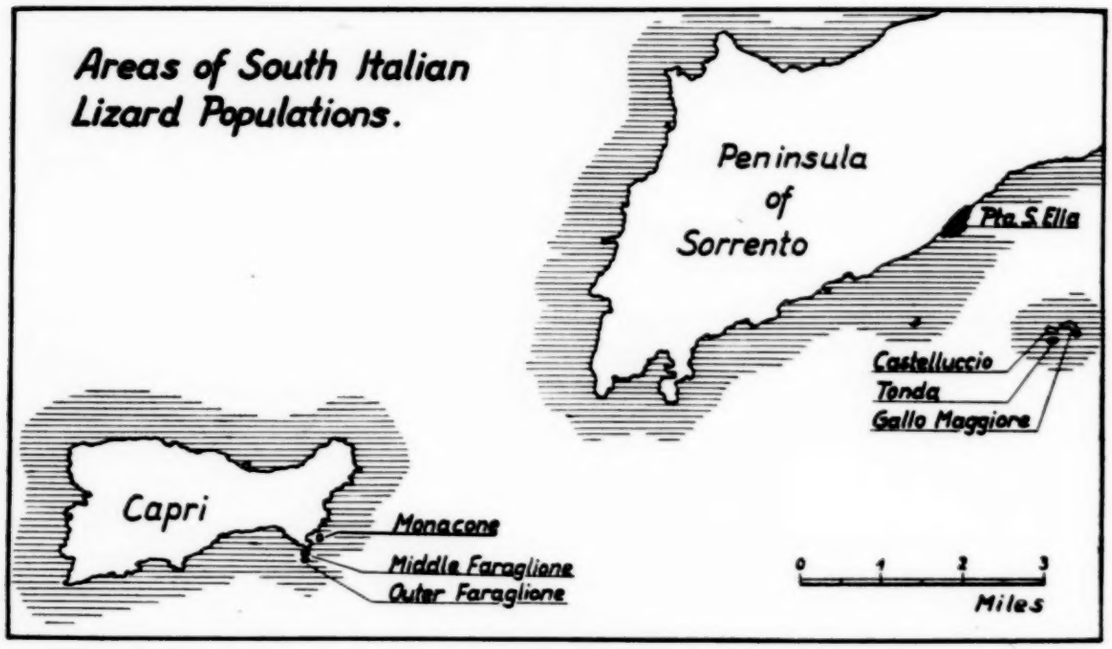

FIG. 1. Areas of South Italian lizard populations.

ever, the great advantage would be forfeited of dependably ascertaining the ancestral continental population.

RELATIVE LENGTH OF THE HIND LEGS (= RELATIVE QUERMAß)

The *"Quermaß"* or span (Kramer and Medem, 1940) is the span of the hind legs measured under certain precautions (cf. loc. cit.) from tip of toe to tip of toe. The relative "Quermaß" or span (abbreviated RS) is established by expressing the actual span of the hind legs in per cent of the head-plus-trunk length (to be abbreviated subsequently as H + T). In employing this index it must be noted that it is subject to an allometric change in the course of growth, for the legs of newly-hatched lizards are relatively longer than those of adults. Allowance for this shifting of form was made partly by comparing newly-hatched individuals, hence

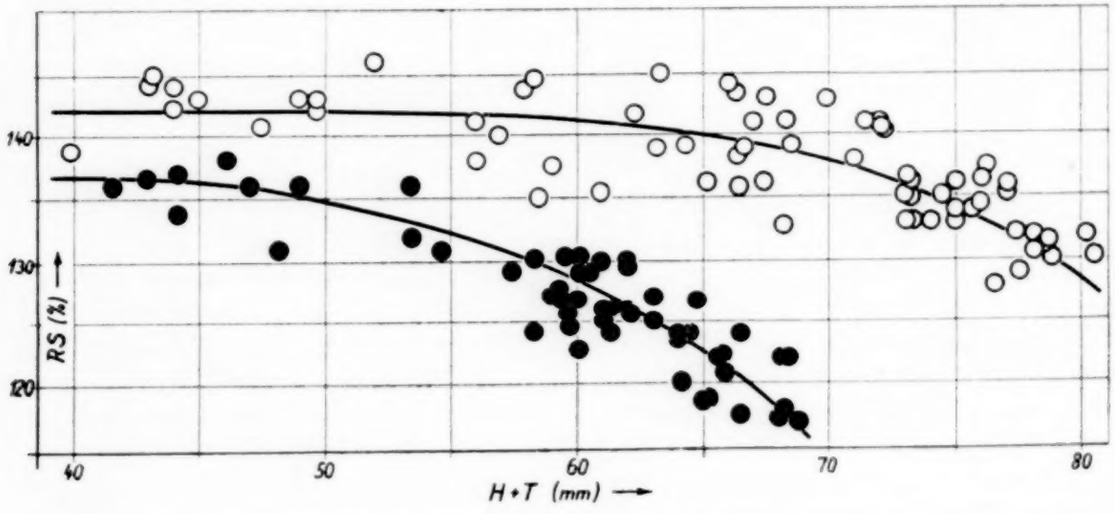

FIG. 2. RS (relative span) of South Italian mainland lizards (Punta S. Elia), plotted against length of head-plus-trunk (H + T). Upper curve (blank circles), males; lower curve (dark circles), females.

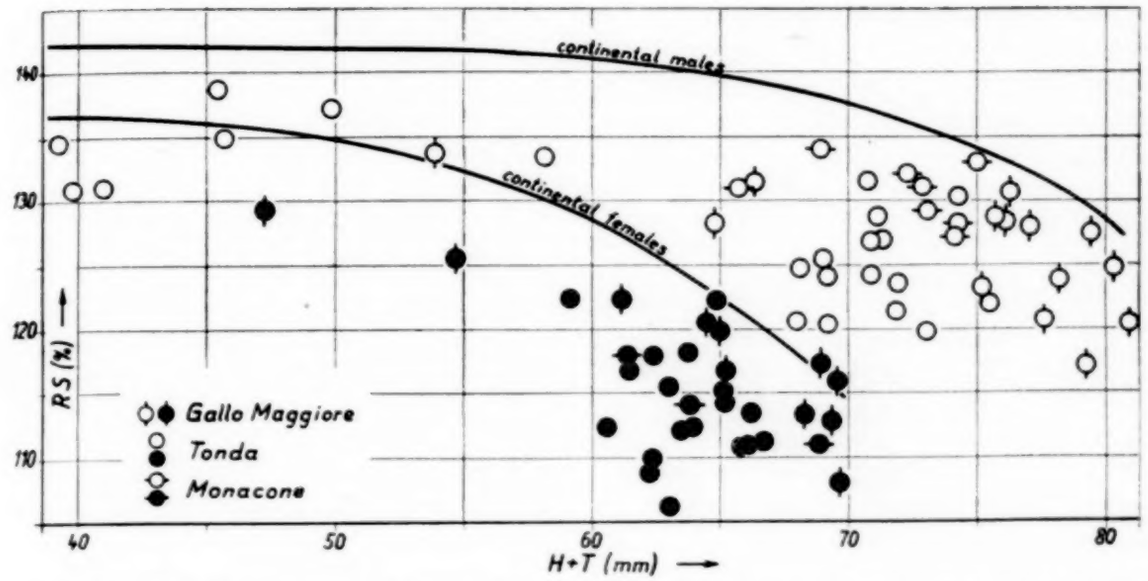

FIG. 3. RS (relative span) of three South Italian island populations, plotted against length of head-plus-trunk (H + T). Blank circles, males; dark circles, females. The curves are those of figure 2 to make possible a comparison with mainland means.

of exactly the same age. Freshly captured lizards were utilized by comparing the empirically obtained curves describing the RS as a function of body size.

Furthermore, RS varies as to sex, males having longer legs than females.

South Italian populations

As a standard continental population the lizards of Punta Sant' Elia on the peninsula of Sorrento (Southern Italy; see map, fig. 1) were selected. In a previous publication (Kramer and Medem, 1940) it has been indicated that two small populations each of the peninsula of Sorrento and of the island of Capri do not demonstrably differ as to their RS. Figure 2 indicates the RS curve for both sexes of Punta S. Elia. (The diagram does not differ fundamentally from the one of 1941; it is, however, corroborated by a considerable number of further single values.)

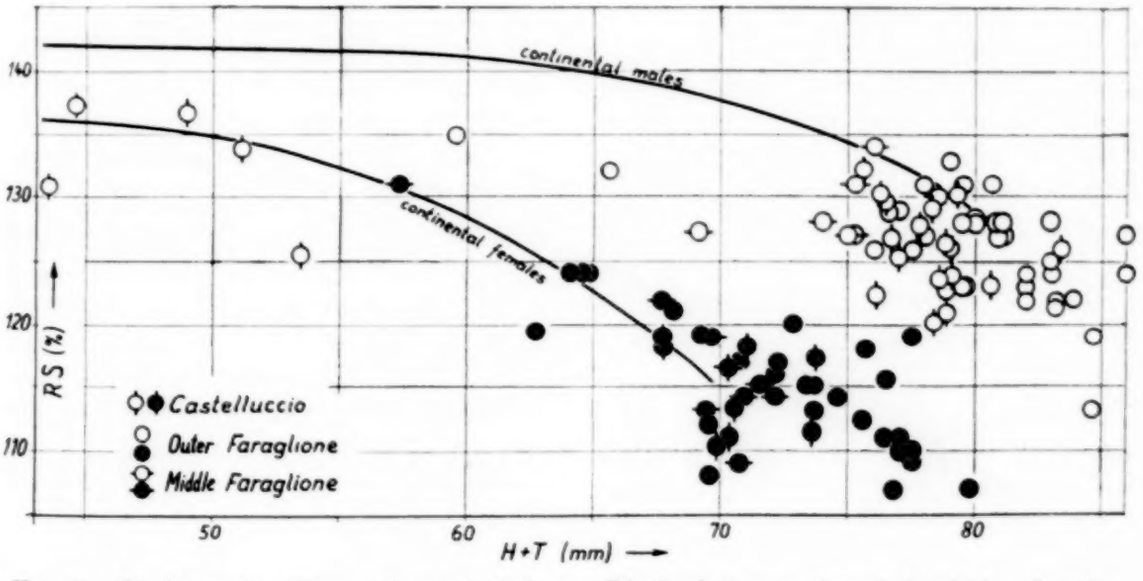

FIG. 4. Cf. figure 2. Three other populations. Blank circles, males; dark circles, females. The curves are those of figure 2 to make possible a comparison with mainland means.

TABLE 1. *RS (relative span) of South Italian mainland and island lizards at hatching stage*

Population	Males (n)	Females (n)	Both sexes (n)
Mainland (Punta S. Elia)	142.0 (9)	137.6 (5)	140.4 (14)
Galli islets			
Gallo Maggiore	135.9 (10)	132.8 (8)	134.5 (18)
Castelluccio	139.2 (12)	133.3 (3)	138.0 (15)
Tonda	135.8 (12)	130.3 (9)	133.5 (21)
Faraglioni rocks			
Outer Faraglione	—	—	136.3 (22)
Middle Faraglione	140.9 (7)	133.5 (4)	138.2 (11)
Monacone	no measurements		

Figure 3 represents those island populations whose lengths of hind legs are considerably below the continental curve: Gallo Maggiore, Tonda (both forming part of the Galli islets off the South coast of the peninsula of Sorrento) and Monacone (the low cliff of the Faraglioni group off Capri).

Figure 4 shows the conditions realized on the three remaining South Italian islands examined in this respect, Castelluccio (Galli group) and the two Faraglioni pyramids (off Capri). The values of the adult males of these cliffs are only inconsiderably below the continental curve, the value of the adult females even slightly above.

Table 1 shows conditions in question with regard to *newly-hatched* young of all South Italian populations examined, Punta S. Elia again serving as the mainland comparison. As the measures obtained on the Outer Faraglione are indiscriminate as to sexes, all calculations had to be made without sex division (last column in table 1). It can be established then that the continental lizards are the most long-legged. The deviation below the mainland mean is statistically secured also for Castelluccio and the Middle Faraglione.[2]

[2] P in these cases is between 0.05 and 0.01; in all other cases $P < 0.01$. Method: Two-criteria analysis of variance, Outer Faraglione exempted as sexes were not considered separately there. The deviation of Outer Faraglione values from those of the mainland was checked with indiscriminate sexes and found to be significant ($P < 0.01$).

Further statistical analysis of South Italian young lizards proves that the relative hind leg values of Gallo Maggiore and Tonda ("group 1") on the one hand and those of Castelluccio and the two Faraglioni on the other ("group 2") may each be considered as statistically "homogeneous." In both cases the variance between was found not to be bigger than the variance within groups. If these two groups are contrasted, the mean RS of "group 1" will be found to be 134.0 ($n = 39$), of "group 2" 137.2 ($n = 50$). The difference is clearly significant ($P < 0.01$).

"Group 1" is identical with the populations represented in figure 3, the adult values of which are considerably below those of the mainland populations. "Group 2" comprises the populations indicated in figure 3, the male values of which are slightly, the female values not at all below the corresponding continental mean.

Istrian populations

The RS's of *adult* individuals of the two Istrian (North Adriatic) insular populations Piroso Grande and Bagnole are smaller than those of the continental ones (Rovigno). The values are sparse (8 island, 8 mainland values); the low island figures are, however, supported by measurements of newly-hatched young: continental mean 131.6 ($n = 18$), Bagnole 127.1 ($n = 7$), Piroso Grande 128.3 ($n = 14$). The differences between the mainland and each of the two islands are statistically significant (P for Rovigno-

Bagnole close to 0.01, for Rovigno-Piroso $< 0.05 > 0.01$).

Influence of different hatching temperatures on relative length of hind legs

The possibility that the difference of leg length might be due to modifying conditions could not be altogether discarded. The stouter forms of the north Italian continental individuals of the species under consideration—i.e. of those coming from a cooler climate—are well defined in terms of the two RS's. They are 131.6 (Istria) and 140.4 (South Italy), without discrimination as to sex in either case. The possibility of a phenotypical dependence owing to a difference of temperature could not be ruled out *a priori*, seeing that similar observations had been made with mammals (Murr, 1933; Ogle, 1934; Przibram, 1925; Sumner, 1932).

The procedure was to hatch half of every clutch at normal room temperature, the other half at 30.8° C. The room temperature varied between 24° and 27° C., some sets of eggs being exposed to temperatures up to 28.5° C. toward the end of egg development.

Even without statistical evaluation the values indicated in table 2 show that there can be no question of hatching temperatures bearing an influence on the RS. Nevertheless the values were subjected to an algebraic examination.

Applying the three-criteria method considering class means only, the differences between sexes turn out to be significant ($F = 30.4$, 1 and 3 degrees of freedom, P somewhat < 0.01); differences between populations slightly significant ($F = 9.55$, 3 and 3 degrees of freedom respectively, P somewhat smaller than 0.05); and the variance between temperature classes proves to be equal to the experimental error. Information improves if the calculation of the experimental error is based upon the single values; in this case clearly significant differences of sex and populations are obtained, experimental error and variance of temperature classes again being practically equal. Treating males alone by means of the two-criteria method yields the same result.

Accordingly the differences in length of hind legs are not caused by temperature. This means practically that direct actions of environmental factors are ruled out. Moreover, these data show that lizards do not respond to changes of temperature, or at least do so in a manner quite different from that of mammals.

It must be admitted that the effective temperatures do not vary very widely, and that the "room temperature" is badly defined. At any rate, the differences in question by far exceed those of the two natural habitats (mainland and islands), if indeed the island climate can at all be assumed to be cooler in June than that of the immediate coastal region (cf. the geographic situation of Punta S. Elia, Fig. 1).

As an additional result of this section it should be noted that sex differences in relative length of hind legs are already pronounced with newly-hatched lizards. Applying the two-criteria method between sex-variance is decidedly significant ($P < 0.01$).

TABLE 2. *RS (relative span) of newly-hatched South Italian mainland and island lizards hatched at different temperatures*

	Males		Females	
Population	30.8°	Room temp.	30.8°	Room temp
Mainland (Punta S. Elia)	142.3 (4)	142.0 (5)	137.3 (3)	137.5 (2)
Galli islets				
Gallo Maggiore	135.8 (5)	136.0 (5)	131.6 (4)	133.5 (4)
Castelluccio	139.1 (7)	139.2 (5)	135.5 (2)	129.0 (1)
Tonda	136.5 (4)	135.5 (8)	130.8 (5)	129.8 (4)

Explanation for the gradation of RS's within island populations

We are confronted with two sets of facts:

(1) In two widely separated areas, South Italy and Istria (North Adriatic), insular races of the same species of lizards show relatively shorter hind legs than the corresponding continental populations. Such shortening of hind extremities can be proved with newly hatched or juvenile individuals of *all* island populations; with adult specimens, however, only in five out of a total of eight cases.

(2) Within the South Italian island populations certain gradations are discernible. The young of Castelluccio, and of the Outer and Middle Faraglione, have longer legs than those of the remaining cliffs (Gallo Maggiore, Tonda); *it is these populations whose adult representatives have hind legs of about the same length as continental specimens.*

If one subjects the South Italian islands to a closer inspection as to their morphologic nature it will at once become apparent that the ones inhabited by long-legged lizards are steeper than the others (see fig. 5). The picture must not create the impression that the populations live only on the tops of the two cliffs. On the contrary, lizards may be found on the precipice 30 to 50 feet above sea level, especially at the east bluff of the Outer Faraglione. (The outer rock is 356 ft., the middle one 264 ft. high.) To provide some means of comparison figure 6 shows Monacone, photographed from the top of one of the high Faraglioni. True, the third of the steep islands, Castelluccio (Galli group), is lower than the two Faraglioni and possesses extended though barren horizontal beach stretches, but, on the other hand, it is considerably higher than its two sister islands (Gallo Maggiore and Tonda) and Monacone, especially in proportion to the base. Among the Galli islets it shows the most marked precipices—a fact that is indeed continually brought home to the collector of lizards. The Castelluccio population is highly instructive in that it cannot be told apart from the Gallo Maggiore population except for the higher RS.

FIG. 5. Outer Faraglione (right-hand side), middle Faraglione (left-hand side).

FIG. 6. Monacone. Photo taken from one of the steep rocks of figure 5.

Looking for factors that might affect the balance of survival of insular as against continental lizards, attention, as usual, is first drawn to the absence, on islands, of enemies whose presence on the mainland tends to keep the agility of the continental animals on a high level.

It hardly will be necessary to give detailed reasons why long-legged lizards are quicker to escape than short-legged ones. Quick snakes (*Zamenis*) which chase lizards *par force* represent a factor selecting for long-leggedness. (I have discussed the question of predation on lizards in my 1946 paper.) This factor is lacking on the islands, and our views as to "degenerative" evolution go to show that a feature brought about by special conditions tends to be regressive if such conditions break down. However, the regressive development, initiated by the absence of predators on the islets referred to, will be slackened in the particular cases where habitat conditions require special climbing agility. A wider range of the legs makes it more likely for a lizard to find footholds on a steep rock, at the same time enhancing its jumping capacity. This explanation is in full agreement with the facts observed here, though of course further investigations are desirable of cases in which lizards live on steep cliffs in the vicinity of flat islands.

RELATIVE LENGTH OF TAIL

Italian populations

The compound values of four South Italian mainland populations seemed to indicate that the relative length of tail (RT) does not change after the end of the first stages of growth, i.e. after H + T = 42 mm.

Surprisingly enough, however, lizards are born with considerably shorter tails. Table 3 evinces, first of all, that the values of older individuals are much higher than those of the young (average with males = 11.8 per cent; females = 9.5 per cent). The increase of RT in the process of growing up can be established without the application of algebraic methods.

A young of diminutive size (male) from the Middle Faraglione, whose dwarf size was caused by chance owing to partial inactivation of the yolk, showed that the relative length of tail has something to do with the size on hatching. H + T

TABLE 3. *Relative tail length of all South Italian lizard populations, distinguished as to age and sex*

Population	Freshly hatched			Older stages		
	Males (n)	Females (n)	Both sexes (n)	Males (n)	Females (n)	Both sexes (n)
Mainland (Punta S. Elia)	196.5 (9)	191.4 (5)	194.1 (14)	236.1 (19)	219.0 (20)	227.3 (39)
Galli islets						
Gallo Maggiore	197.9 (10)	189.5 (8)	194.2 (18)	222.5 (6)	204.0 (3)	216.3 (9)
Castelluccio	198.1 (12)	192.7 (3)	197.7 (15)	212.5 (2)	213.0 (2)	212.8 (4)
Tonda	197.8 (12)	193.4 (9)	196.0 (20)	225.0 (11)	206.3 (3)	221.0 (14)
Faraglioni rocks						
Outer Faraglione	—	—	195.6 (20)	213.0 (2)	191.8 (2)	202.4 (4)
Middle Faraglione	193.3 (7)	182.0 (4)	189.2 (11)	202.0 (4)	198.5 (2)	200.8 (6)
Monaccone	—	—	—	233.0 (1)	—	—

was 24.4 mm., as against an average of 32.3 mm. with specimens of a normal size. RT was 156 per cent as against 190 ± 2.0 per cent. Thereupon an investigation was made to find out if such a correlation also applied to newly-hatched young within the normal range of size variability. Part of the populations had to be eliminated as unsuitable owing to small variability of H + T. With other groups, however, the dependence of RT on the size at hatching stage could be clearly confirmed, especially with Tonda males.

Any attempt to prove a similar relation between the mean values of the various populations is bound to fail, simply because every population has its cursive adult RT value. This share of the variability due to the specific proportions of each population and disguising the dependence of the hatching RT on the size can, however, be eliminated by isolating the *increment* that equals the difference of mean RT of adults and the mean RT of young, expressed in per cent of the latter. The result clearly to be inferred from figure 7 can be expressed as follows:

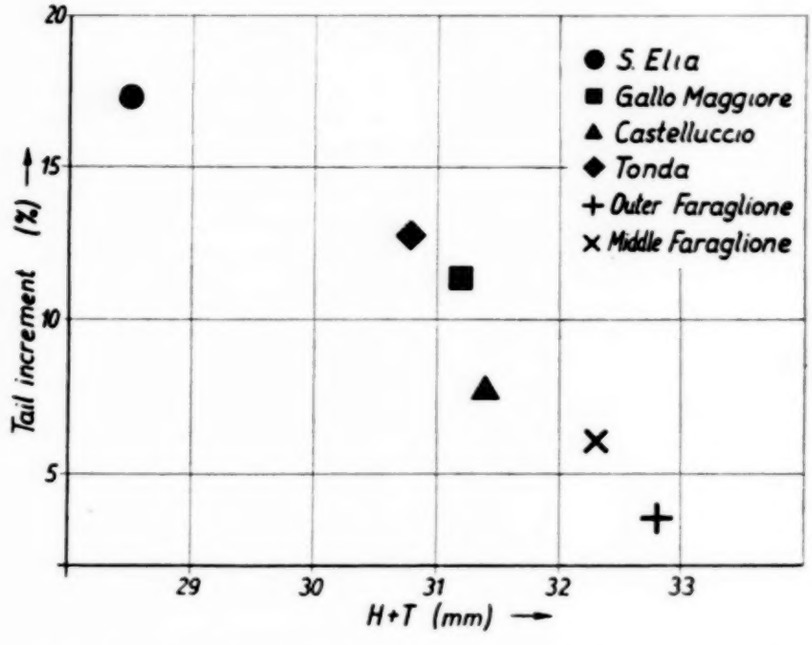

FIG. 7. Tail increment (= increase of relative length of tail during growth, expressed in per cent of relative tail length, RT, at hatching), plotted against size at hatching stage. All South Italian populations.

TABLE 4. *Deviation of relative tail length on Islands from relative tail length on Mainland, expressed in per cent. The table shows that some insular lizards have longer tails at hatching stage, but that at later stages they all have shorter tails than mainland specimens*

Population	Newly hatched		Older stages	
	Males	Females	Males	Females
Gallo Maggiore	+1.2	−1.0	−5.8	−6.9
Castelluccio	+1.3	+0.7	−10.0	−2.7
Tonda	+1.1	+1.0	−4.7	−5.8
Middle Faraglione	−1.2	−4.9	−14.5	−9.4

The bigger the hatching size of a population (H + T at hatching stage), the less its RT at hatching stage will differ from its ultimate RT.

It may be mentioned here that the dwarf required the same hatching time as any normal egg, which goes to illustrate plainly that the rate at which RT reaches its ultimate stage is not a function of the time element but rather a question of the building material available—at least up to this limit.

Similar to the relative length of hind legs, the relative length of tail was checked as to the direct influence upon it by temperatures. *Here as there, the result was negative.*

If on the strength of the values for the young the variance between sexes is represented together with the variance for comparison of populations, high significance is obtained. As with the length of hind legs, the young lizard is also differentiated as to sex with regard to the length of its tail.

So far we have only dealt with newly hatched animals. As to adults, a glance at table 3 will show that sex differences are manifest in the same way as with newly hatched specimens; their scope may be even bigger, though scattering is considerable and too few single values are available to warrant definite establishment of the increase of sex differences. On the other hand, the relation between mainland and island values has undergone a change. While there is a definite though not certifiable suspicion that RT is increased with part of island young, as can be inferred from table 4, the corresponding values of adults show a marked *decrease*, which is statistically secured for all populations included in this table.

The scarcity of single values is due to the frequency of automized tails. On islands the percentage of broken tails is even higher than on the mainland, owing to greater density of population and ensuing frequency of fighting.

Istrian populations

Both newly hatched and old lizards of the islands of Piroso and Bagnole have shorter tails than the same age groups of the continental race (table 5). For corroboration of sparse adult values, cf. measurements carried out by Mertens (Kramer and Mertens, 1938), which on principle indicate the same phenomenon. Further on it is statistically established that the relative reduction of tail length is more pronounced with young individuals from Bagnole than with those of Piroso, no plausible explanation being available.

The connection between size at hatching stage and increment to be afforded (cf. fig. 7) as ascertained with South

TABLE 5. *Relative tail measure of newly-hatched and older West Istrian Mainland and Island populations*

Population	Young (both sexes)	Older stages	
		Males	Females
Mainland			
Rovigno	171.5 (18)	199.5 (4)	184.3 (3)
Bagnole	149.2 (7)	185.0 (1)	163.0 (1)
Piroso Grande	162.3 (14)	159.0 (1)	146.0 (1)

Italian material is confirmed by the behavior of lizards from Piroso, though not by Bagnole ones; in spite of the fact that their size at hatching stage is considerable if compared with continental lizards, the relative length of their tails is, from the first, as small as that of adults. There are no evident reasons for this phenomenon.

Relations of relative length of tail to absolute body size and number of tail vertebrae

With reference to adult individuals, the general statement applies that island lizards have relatively shorter tails than continental ones. As this applies with certainty to seven out of eight island populations, with the eighth (Monacone) in no way disproving it, it may be considered generally applicable (cf. also Kramer and Mertens, 1938).

With regard to newly-hatched individuals the comparison between island and continental lizards shows varying results. After establishing a definite dependence of the relative tail increment to body size at the stage of hatching maturity (cf. above, page 200), it must be considered merely fortuitous whether or not an island lizard at hatching stage has a relatively longer or shorter tail than a continental one. Our statement then must be this: at a very early post-embryonic stage, the fact that island lizards have shorter tails may be obscured by the fact that part of the early increment in tail length is anticipated within the egg, owing to the bigger supply of yolk in the island egg. The experiment of hatching short-tailed island dwarfs by inactivating part of the yolk has been anticipated by chance.

A number of hybrids at hatching stage (Outer Faraglione female × mainland male) showed an even higher RT than pure-bred Faraglione young. Now, the hatching size of the young is determined only by the P-female, which means that these hybrid hatchlings were as big as pure-bred Faraglione young. Assuming complete or partial dominance of the alleles determining long tail in the final body form, the above paradoxical effect would be explained. The difference of the two means (198.6 [n = 15] versus 195.6 [n = 20]) does not prove to be significant, on the basis of measurements hitherto available.

Further enlightenment may be expected from the structure of the skeleton of the tail. The tail of a lizard is verticillate, and it is conspicuous that one longer verticil is always followed by a slightly shorter one. The fact that two verticils form a pair each is accounted for by the fact that one pair always is supported by one vertebra, as can easily be ascertained by sectioning. Accordingly there is a fixed relation of 2:1 between verticils and vertebrae, making allowance for small inaccuracies in the immediate post-anal region and at the outermost tip.

Counting technique

The posterior lip of the anus is covered with small irregular scales which are not counted. The first all-round ring of scales is considered the first verticil. As to the distal region there are no doubtful points, except whether the tail is intact or not. Tails that were broken off at an extremely distal point are hard to recognize as regenerates, even if the transition to the incompletely ossified spine can often be felt between two fingers.

The first fact to be noted is that, barring loss and regeneration, the number of verticils remains constant during the whole of the post-embryonic development.

Table 6, distinguished as to sexes, shows that there is no sex difference, at least not within the limits of accuracy imposed by the material available. It further shows that the two Istrian island populations, in keeping with their shorter tails (cf. table 5), exhibit a decrease of the number of verticils and, accordingly, of vertebrae. (Analyzing the figures of table 6 by two criteria yields high significance for population differences.)

The number of tail verticils of the dwarf from the Middle Faraglione is 103,

TABLE 6. *Number of verticils of West Istrian Mainland and Island lizards, distinguished as to sexes*

Population	Males	Females
Mainland Rovigno	105 (7)	105 (10)
Bagnole	91 (5)	94 (2)
Piroso Grande	98 (7)	96 (5)

i.e. exactly the same number as with his normal population fellows. His relative length of tail was 156 as against the normal male average of 192. This goes to show clearly that the determination of the number of vertebrae is independent of the supply of substance, though the latter exerts a decisive influence on the length of the tail.

Ecological importance of tail length

No extensive study has been made so far of the function of the lizard's tail in locomotion. The fact that it is essential follows from the observation that lizards without a tail can be more easily caught, at least if moving on level ground, than those with a long tail. I have reason to believe that lizards if moving through grass make no use whatever of their legs and proceed by means of undulating movements like snakes or the limbless lizard, *Anguis*. Nothing definite, however, can be said without cinematographic evidence. (When running on *bare* soil, the lizard eliminates its tail as a means of locomotion by lifting it. The axis of the lizard is then rigid all the way through and the legs alone do all the work. Only when changing direction, the tail is violently waved.)

Accordingly a long tail will be more useful for locomotion than a short one. The reduction in tail length in island animals is therefore just as intelligible as that of the legs.

At first glance these speculations about the part played by the tail in the survival of the species seem to be contradictory to the fact that the lizard so easily and frequently parts with it by means of autotomy. It must be pointed out, though, that autotomy of the tail is a highly effective method of protection from predatory enemies. No matter how vital the tail may be for purposes of locomotion, it is better to lose it than to die. Similarly the fact that the chilopod *Scutigera* throws off its legs if seized will not lead anyone to the conclusion that they are unimportant for him. In both cases the vital importance is indeed emphasized by the fact that the autotomized limb or tail will be regenerated.

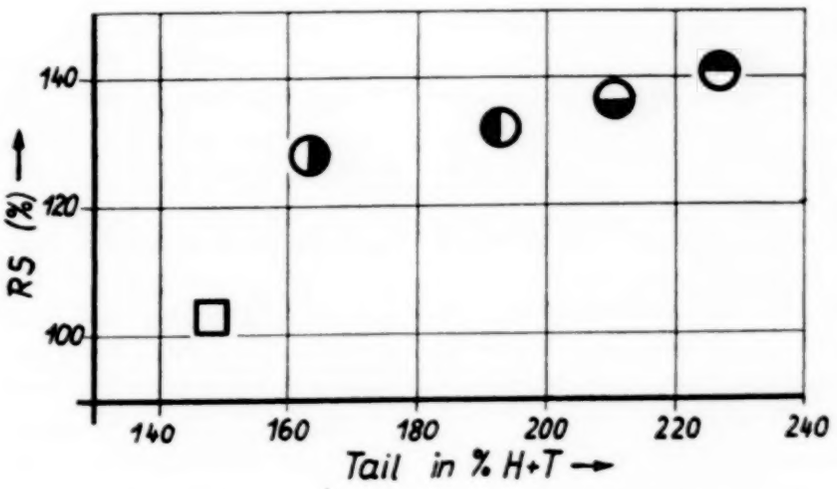

FIG. 8. Correlation of RS and RT. Circles, *Lacerta serpa*. Decreasing RT: South Italian mainland, South Italian islands, West Istrian mainlands, West Istrian islands. Square: *Lacerta agilis*.

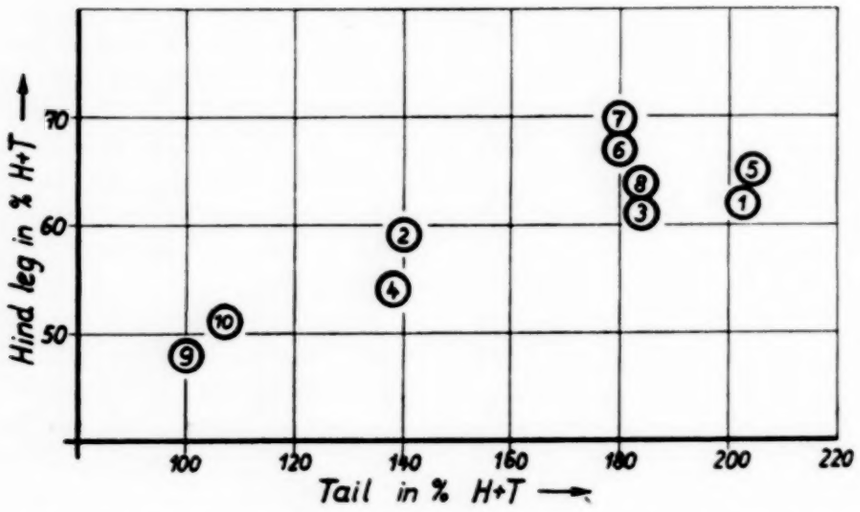

FIG. 9. Relative lengths of hind legs and tail of South American *Iguanidae* (genus *Liolaemus*) according to measurements by Hellmich (figured in per cent of head-plus-trunk). (1) *Liolaemus m. monticola*, (2) *Liolaemus m. villaricensis*, (3) *Liolaemus a. altissimus*, (4) *Liolaemus a. arancanicus*, (5) *Liolaemus chiliensis*, (6) *Liolaemus t. tenuis*, (7) *Liolaemus m. monticula*, (8) *Liolaemus a. altissimus*, (9) *Liolaemus magellanicus*, (10) *Liolaemus nigromaculatus bisignatus*.

THE CORRELATION BETWEEN RT AND RS

As all island populations under examination have both shortened hind legs and shortened tails (the latter with the one reservation made in the case of Monacone), there exists such a correlation within each of the two areas (South Italy, Istria). It is evident from what has been said so far that such a relation can be established also in a comparison between the North Italian and South Italian continental races. The data are compiled in figure 8.

I have also included the stout *Lacerta agilis* in the same figure. It can be inferred from this that the correlation as suggested also applies interspecifically, even though the hind legs of *L. agilis* are shortened to a higher degree than the tail. The same follows from figure 9, in which Hellmich's data about Chilian *Liolaemus* species are arranged on a pattern similar to that of figure 8.

Subsequently, all suitable material (nine groups) was graphically examined for a correlated variability of length of tail and span with individuals of the same population and belonging to a well-defined age-group (the only choice in this respect being the hatching stage). The result was negative, which seems to indicate that this relation, which was established in a comparison of various races and species, constitutes a result of environmental selecting influences working in the same sense on two features that vary independently of each other.

DISCUSSION

Island effects

In connection with the several sections of this paper we have already discussed an interpretation of the shortening of limbs and tail in the insular environment as symptoms of adaptation, more accurately speaking, as the outcome of a "regressive" evolution owing to a slackening of demands upon locomotion.

We must not forget, though, that in populations of a limited number of individuals one must also look for the effect of chance fluctuations in the frequency of alleles. But as the "quantitative" features dealt with here are presumably controlled by several genes each, and as every pair of alleles is independently subject to

the effect of genetic drift, no phenotypically visible effect can reasonably be expected. Different behavior of populations will rather have to be accredited to differences of habitat features or geological age of the islands.

Similarly, a narrowing of variability range, which might more likely have been expected, cannot be proved. In all suitable cases we have checked the σ-values, both of the relative length of legs and tails, and have *not* been able to detect any decrease on islands.

Allometric shifts

Apparently deviating from the antero-posterior growth ratio which can be generally stated in the development of vertebrates, we find that the hind legs of the lizard reach their maximum relative length with the newly-hatched animal. This has its counterpart in the proportions of newly-hatched birds: newly-hatched gallinaceous birds (*Galli*), waders (*Limicolae*), or cranes (*Grues*) are distinctly long-legged. Young storks (*Ciconiiformes*) or herons (*Ardeae*), on the other hand, grow the better part of their hind extremities during their nestling period.

Hoofed mammals (*ungulates*) show even more marked relative lengths of extremities when newly born than as adults (see J. Hammond in Zuckermann and others). By way of contrast, compare the juvenile development of a dog which is born stump-legged and does not reach its final body proportions until it is fully grown or shortly before. In all the instances of vertebrates listed above we are faced with a premature growth of extremities in keeping with such other peculiarities as warrant immediate efficient locomotion of the animal with its final, non-larval locomotory organs. This kind of specialization naturally has its consequences for the embryonic period in which the birth stage must be prepared.

Analogous to the above mentioned conditions with ungulates, we find a *regression* of the relative length of legs among lizards in their later stages of development. With the inhabitants of steep cliffs (the two Faraglioni and the Galli islet Castelluccio) this decrease is moderated. —As Huxley would put it, the hind extremities of lizards show a negative allometric growth. Rensch especially has referred to such shifts in proportions in order to explain evolutionary changes of proportion (allomorphosis [3]). Accordingly it might be expected that, within a related group, big species of lizards generally would have shorter legs than small ones. To examine this point at greater length would exceed the scope of this paper.

As to the tail of the lizard, however, we discovered that its ultimate length is not reached at hatching stage. With island races, which have a bigger hatching size, the relative length of the tail is closer to the ultimate proportion than with continental races. We are faced here with an early allometry which must be distinguished from such late allometric changes as that of the length of hind legs. This is already indicated by the speedy attainment of the maximum of the relative length of tail. In this case the quantity of reserve substance available could be shown to act as a restrictive factor. In accordance with the rule of antero-posterior preferential growth, the tail suffers as less yolk is available. Mechanisms involved in allometric shifts consisting in variations of yolk supply and evidently affecting only juvenile stages, can hardly be expected to play a part in evolutionary processes. I propose to call changes produced in a similar way "early allometric shifts."

Summary

In two separate areas (Tyrrhenian area, Southwestern Italy, and Western Istria, North Adriatic), island populations of the lizard species *Lacerta serpa* (= *sicula*) show a relative shortening of hind legs at hatching stage. In the case of adult island lizards the same shortening is demonstrable with populations in-

habiting *flat* islands. Equally, the hind legs of the latter are *more markedly* shortened at hatching stage than those of the inhabitants of steep cliffs. The shortening of hind legs is accounted for as a regressive change in adaptation to the reduced demands on locomotion in insular environment (no predators). On steep cliffs, the regression appears to be less marked owing to an increased demand on climbing ability.

All island populations examined have shorter tails than continental ones, a fact that is equally accounted for as a locomotor regression.

Lizards hatched at different temperatures behave the same with regard to relative hind leg and tail measurements.

The number of tail vertebrae (measured by the number of verticils, two verticils each associated to one vertebra) is higher with continental lizards than with insular ones. The determination of the number of vertebrae is independent of the quantity of yolk material available. The *length* of tail with newly-hatched lizards, however, clearly depends on the quantity of reserve substance. The tails of such populations as lay big eggs (island populations) therefore require less growth in post-embryonic stages than the tails of populations laying small eggs. (An exception to this rule is formed by one of the two Istrian island populations.)

In inter-specific comparison, relative length of tail and length of legs are correlated. Such a correlation cannot be established in intra-specific comparison.

There is no indication that the intra-population variability of the features examined is restricted by the effect of small population numbers.

The relative growth of hind legs and tail makes possible a distinction between allometric changes in early and later ontogenetic stages. Presumably the latter only can be considered indicative in a sense of evolutionary allomorphosis.

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EVOLUTION OF THE EARLY TERTIARY RODENTS

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INTRODUCTION

Representatives of the order Rodentia first appear in the late Paleocene (Tiffanian) deposits of the Fort Union Series. The known material is, however, exceedingly fragmentary, for only a single lower molar tooth and some incisors have been found. The specimens have been referred to the genus *Paramys* (*sensu lato*). They demonstrate that the characteristic rodent incisor and molar were already developed at the time. These teeth suggest that most of the other characteristic rodent features were also present, although it is, of course, possible that some primitive features absent in other rodents were still retained. *Paramys* (*sensu lato*) is relatively well known from the early Eocene (early Wasatchian) deposits of the Willwood formation, and similar rodents are known from the early Eocene of Europe. In their comparable parts, these later rodents do not differ in any important respect from the late Paleocene species. All rodents known from the late Paleocene and early Eocene pertain to the superfamily Aplodontoidea and to the subfamily Paramyinae (or family Paramyidae of other authors), the most primitive group of rodents.

These early paramyines are nearly structurally antecedent to all later rodents, if indeed they are not their actual ancestors. Primitive as they are, they already have acquired the formally diagnostic characters of the order insofar as skeletal structures are concerned; and these characters, fully developed, show no transition to those of the Insectivora (*sensu stricto*), or to any known primitive placental.

Several early insectivore or primate groups (mixodectids, apatemyids, *Phenacolemur*) exhibit some degree of convergence in the incisors and lower jaws toward a rodent type of structure. Osborn years ago placed the mixodectids in a distinct suborder of ancestral rodents, the Proglires (Osborn, 1902, p. 203). Further detailed examination has failed to reveal any evidence for such a relationship. Structures common to the mixodectids (presumptive insectivores) and rodents are shown also in several other groups which have no special relationship to the Rodentia. The apatemyids and *Phenacolemur* are regarded currently as probable primates. It seems that in the early Cenozoic several placental groups had similar adaptations of the front teeth with attendant, correlated modifications of the jaws. Perhaps these groups indicate a series of competing forms which finally passed to extinction as the rodents slowly rose to ascendancy.

Many workers have accepted the conclusions of W. D. Matthew (1910), and have followed his thesis that the paramyines are actually ancestral to all later rodents, and that rodent diversification in the higher categories has been a post-Paleocene event. Others, particularly Miller and Gidley (1918), have at least implied that the known stratigraphic record is faulty, and that all major groups of rodents (approximately the superfamilies of the Miller and Gidley classification of 1918) were in existence by early Eocene time.

Advocates of Miller and Gidley's view perhaps tend to think of the origin of the order as occurring at an earlier time than do those advocating an Eocene diversification. According to various suggestions, the time of origin may range from far back in the Cretaceous to early Paleocene. If we accept one of these dates, particularly a Cretaceous one, and agree

with Matthew as to the Eocene history of the rodents, it is remarkable, as A. E. Wood has said (1937, p. 222), that such a long time elapsed before any major taxonomic diversification took place within the order. It is not until late Eocene that demonstrably non-aplondontoid rodents appear.

I have reviewed in another place (1949) most of the Eocene and post-Eocene evidence in support of Matthew's conclusions. Here it need only be stated that such stratigraphic information as is available supports them—a not too surprising result, for it was largely on this basis that the theory was built. The post-Paleocene evolutionary picture developed under this view is not an exceptional one, being essentially the same as, for example, in the Artiodactyla. It has one point of similarity also with that of the Carnivora and Primates: the modern superfamilies, as definitively recognizable groups of these orders, seem to arise from archaic groups at approximately the same time (around the Eocene-Oligocene boundary). If we accept an Eocene date for primary differentiation within the order (and I think the fossil record as now known suggests no other date even if it does not prove it), the problem of time of origin is still left untouched, except that a later date for differentiation suggests a later date for origin of the rodents.

Geologic Record of the Continental Paleocene

The salient facts concerning the stratigraphy of the continental Paleocene should be reviewed briefly. These facts indicate that little direct evidence bearing on the evolution of rodents is likely to be forthcoming from the Paleocene in the near future, and also show the relatively frail foundation for any observations that can be made.

Only in the Rocky Mountains of North America is a reasonably complete and fossiliferous section available for study. Here we do have a sequence which can stand as representing lower, middle, and upper Paleocene. Of these stages, perhaps the fauna obtained from the middle Paleocene (Torrejonian) is the best known. It is, I think, a reasonably good sample of the life of that time in North America. Elsewhere we find no rocks, or more exactly, no faunas which represent the continental lower and middle Paleocene. It is not until late Paleocene time that mammalian faunas other than North American are known, and even then these are from small areas and incomplete. In this interval, "faunas" have been obtained from Outer Mongolia, Europe, and probably South America. No rodents have been found in these beds, but the faunas are too poorly known to admit the supposition that the order was then restricted to North America. On the other hand, the fauna of the North American middle Paleocene has been obtained from surface as well as quarry sites, and over an area including parts of Montana, Wyoming, Utah, and New Mexico. The absence of rodents from the extensive microfaunas indicates absence of the group from North America at the time, although the rather recent discovery of rodents in the Tiffanian suggests some caution in accepting this conclusion (Jepsen, 1937, pp. 293–294).

Evolution of the Mammalian Orders

However the early history of the rodents be interpreted, it is true that an unbridged gap separates the order from their placental ancestors. This structural gap is not unusual, for few connecting links exist between major divisions of the mammals, or of the vertebrates in general (Simpson, 1944, pp. 105–107). These discontinuities have been explained in various ways.

First, it has been maintained that the breaks are the result of a defective stratigraphic record. Regardless of the size of the taxonomic units concerned, evolution proceeds throughout at much the same rate and with much the same material. The early and long-enduring transition stages have simply not been recovered.

If this be true, it is remarkable that the initial stage in the evolution of a group should be so universally affected by deficiencies of record. The theory almost necessitates relatively small numerical representation during the early history of most groups.

Second, it is believed by some that evolution in the higher categories proceeds by tremendous leaps in organization. Rodents, for example, came into being almost instantaneously, geologically speaking. There is no good explanation of how this can be accomplished, especially as a population phenomenon. In any case, the occasional presence of intermediates shows this cannot be a universal means.

Last, it has been proposed that the processes which produce major adaptive shifts in populations are the same as those for the evolution of all grades. The population involved, however, is out of equilibrium with its environment, and consequently the selective pressure is high. It must then modify rapidly or fail entirely. Presumably, such shifts are effected by small or moderate populations under isolation, which thus reduces the chance of recovering a fossil record. Of the three theories, the last seems in best agreement with what little data we have available for the rodents. If we accept it, the development of the typical gliriform incisor of persistent growth could have been rapid in terms of geologic time. Many other features of rodent morphology are correlated with this structure, and might likewise have been rapidly acquired.

Most of the mammalian orders were in existence by the close of the Paleocene. Few are actually known from the late Cretaceous (Multituberculata, Marsupialia, Insectivora). Insofar as an exceedingly scant stratigraphic record is concerned, the placental orders, other than the Insectivora, are the product of post-Cretaceous evolution. Some differentiation among the placentals at the beginning of the Paleocene is also a matter of record. Hence greater differentiation than we observe from the Cretaceous fossils must almost certainly have taken place before the close of that period. Many placental orders probably did have their origin in the Late Cretaceous—some, however, in post-Cretaceous time. The rodents must have had a generally similar history, and might well have become differentiated from their parent stock within Paleocene rather than Cretaceous time.

Antiquity of the Rodentia

It has been suggested by Jepsen (1937, pp. 291–292, 301; see also Wilson, 1949, p. 92) that the finding of typical rodents in the late Paleocene supports the conjecture, one held perhaps by most workers, that initiation of the order occurred "at least as early as Cretaceous time," and that the Rodentia are among the most ancient of mammals. Both these statements may be true, but it is also possible that relatively rapid evolution took place prior to the late Paleocene. We have no direct criteria for judging. The real time of origin is of course not changed by this evidence, only our opinion regarding a probable time. If we were judging by various other Paleocene genera, could not we make much the same statement about most mammalian orders? Even in the earliest Paleocene (Puercan), the ferungulate cohort was at least imperfectly separated into carnivores and ungulates. What we know of the geologic record of the early unguiculates, in comparison with the ferungulates, points to a greater divergence at comparable time levels of the groups making up this cohort; and thus suggests greater antiquity for its various orders (and especially for the subdivisions of the Insectivora).

I do not see that there is any real evidence that the rodents are geologically older than the various subdivisions of the insectivores, the primates, taeniodonts, edentates, cetaceans, or the ferungulates as a group. The Rodentia may be of somewhat later origin than most orders. Primates, taeniodonts, fissipeds, condylarths, and pantodonts all appear earlier

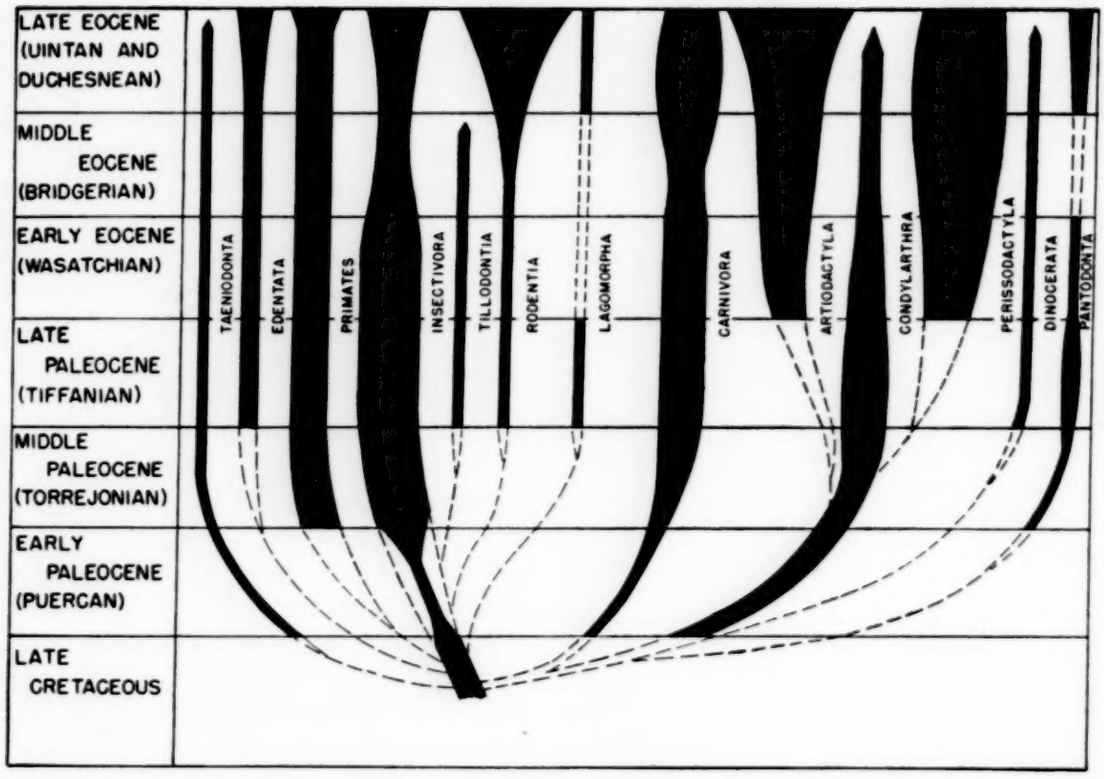

FIG. 1. Stratigraphic and phylogenetic relationships of some orders of placental mammals. The width of each stem has been drawn so as to be proportional to the number of recognized families; hence, width is an approximate measure of the degree of differentiation within an order. Authority for range and number of families is Simpson, 1945.

than the first rodents, and tillodonts and edentates at the same time. The differentiation within primates at comparable time levels is much greater than in rodents, and some of these (*Labidolemur*, *Phenacolemur*), if primates at all, are essentially as specialized in dentition as is *Paramys*. *Didymictis* (middle Paleocene-early Eocene), if it is to be considered as a real fissiped, suggests considerable age for the modern division of the Carnivora. It is, of course, possible that the varying degrees of divergence from the central stock are the result of different rates of evolution rather than any real difference in time of origin; but this hypothesis suggests equal duration for the placental orders, not greater age for the rodents. In the absence of factual data on which to base a judgment, it is perhaps more reasonable to assume generally constant rates at comparable taxonomic levels.

Yet, are we, in any case, willing to admit, as some have strongly maintained (e.g.: Gidley, 1915, p. 402; 1919, p. 275), that in Cretaceous time, more specifically late Cretaceous time, a diversified mammalian fauna existed in which many orders were represented in more than their rudimentary beginnings? When we speak of orders of the Paleocene, we are apt to maintain concepts taken from the Recent fauna in which mammals are much more strongly differentiated at an ordinal level. The bulk of the Paleocene mammals are, after all, morphologically quite similar. If we knew nothing of mammals after the Paleocene, we could well include most of them in a single order. Their Cretaceous ancestors would be extremely difficult to separate, and no vast amount of time is needed for their divergence. Our very meager Cretaceous record of placental mammals does not indicate diversity, other than a modest amount at an insectivore level, and the ascendancy

of reptiles seems to contradict this diversity indirectly. It is, of course, a matter of record that some differentiation of the mammals had taken place by early Paleocene time, but this may have been accomplished in rather late Cretaceous time in areas presumably other than North American.

The collapse of the reptilian dynasty probably gave the mammals an unusual opportunity for rapid exploitation of the earth's surface. In this connection, it is obvious that the populations of Mesozoic reptiles did not all become extinct at the same moment, and that the Late Cretaceous was a long period of time, presumably at least as long as the combined Paleocene-Eocene. As the characteristic Mesozoic reptiles passed to extinction, certain local areas may have become centers favorable for mammalian exploitation long before others (long in terms, say, of subdivisions of Paleocene time). This statement is probably valid if we may assume that the rise of the mammals resulted largely from failure of the reptiles rather than that mammalian success caused the decline of the typical terrestrial reptiles of the Mesozoic. If there were such areas, they are now without preserved deposits, or are unexplored.

If, then, there is no really factual evidence to demonstrate the great antiquity of the placental orders, or to demonstrate the relatively greater antiquity of the Rodentia as compared with them, is there any evidence which would tend to place the origin of the rodents in time, at least in respect to the acquisition of the chief defining characters? I think there may be.

Multituberculates and Rodent Evolution

In view of our lack of direct knowledge of middle Paleocene rodents, or their ancestors among the Insectivora, it is perhaps permissible to search for any indirect evidence which may be forthcoming in respect to the pre-Eocene history of the group. This history poses two related questions: (1) when did rodents originate; (2) are data available from the Cretaceous and Paleocene to substantiate the evidence of post-Paleocene rodents that differentiation within the order is middle Eocene and later? These questions can scarcely be discussed entirely separately, for it is evident that if origin of the order is approximately late Paleocene in time, differentiation must be mostly post-Paleocene; if considerably earlier, differentiation probably, although not certainly, occurred at an earlier time. Conversely, if Eocene differentiation is a fact, then a relatively late origin of the order is strongly suggested in the absence of direct evidence to the contrary.

In regard to these questions, some aspects of the history of the Multituberculata may be instructive, especially as set forth by Jepsen (1949, pp. 488–489). The Multituberculata first appear in the Late Jurassic of Europe and of North America. They last appear, so far as we now know, in the early Eocene (middle Gray Bull, to be perhaps overly precise: Van Houten, 1945, p. 448) of the latter continent. These mammals exhibit in their jaws and teeth a superficial resemblance to the rodents, and they seemingly had rodent-like habits. The enlarged incisors show various stages of development from those with enamel-covered and pointed crowns to those with restricted enamel bands and almost chisel edges. Probably none reached a stage where the incisor had persistent growth as in rodents. With enlargement and specialization of the incisors a diastema developed and, in the lower jaw, a considerable reduction of the premolar dentition took place. The molars have a characteristic pattern of two or three rows of cusps, superficially like that of typical murid rodents. Lastly, the range in size approximates that seen in rodents. The resemblance, particularly in the molars, is sufficiently great to have led some workers to express the opinion that the multituberculates were, in fact, ancestral to the rodents. What is to be regarded as overwhelming evidence, however, shows that

this is not true. Rather, the multituberculates took the place of rodents in the earlier mammalian faunas, but had no other relationship; the resemblances are the result of convergence owing to at least roughly similar modes of life.

The stratigraphic record of the multituberculates suggests that they were replaced ecologically, and rather rapidly so, by the rodents (*ibid.*). Multituberculates must have been common animals throughout the Paleocene over most of the world. They are present in every large collection made by surface collecting in North America, and are found in large numbers in most of the Paleocene quarry collections. Beyond this continent, they are known from two of the three areas yielding late Paleocene mammals—that is, eastern Asia and Europe. Only in South America is the record negative. The Polydolopidae have been thought to represent the order, but Simpson (1928) has shown that this South American family is a marsupial group, presumably of aberrant caenolestids. Presence of multituberculates in the faunas of such widely separated localities of the late Paleocene suggests that they existed in considerable numbers everywhere in the northern hemisphere. Especially is this indicated by their presence even in the relatively meager mammalian faunas of Asia and Europe. We do not know what the situation was in respect to Australia and Africa. In contrast, only a few fragments of rodents have been found in the upper Paleocene, all from the Fort Union of Montana and Wyoming. In the early Eocene numerical representation is reversed. Rodents are fairly common in deposits of this age in North America, and are known also from Europe. Early Eocene multituberculates, unlike rodents, are quite rare, and have been recovered only from the Willwood formation of the Big Horn Basin.

What is meant by a common fossil is, of course, somewhat arbitrary, but it has been my own experience that rodents can be obtained from almost any large exposure of early Eocene age in the Big Horn Basin of Wyoming. They are more common here than multituberculates are in the middle Paleocene of the San Juan Basin of New Mexico. No rodents are known from Asia, but neither are any other mammals of early Eocene age with a few possible exceptions.

If, as seems possible (Simpson, 1947, p. 659), Europe and North America were at this time connected only by way of Asia, the faunal resemblance between the two suggests a continuous faunal sheet across Asia which would include rodents comparable in general to those actually found in Europe and North America. Although the only Paleocene fauna actually known from Asia (the small faunule from the Gashato formation) is not much like either the late Paleocene fauna of North America or of Europe, it may be postulated that faunal resemblance was also marked in late Paleocene time. In view of the pronounced similarity of faunas in the early Eocene, extrapolation of meager data is not so reckless as it would be for a later time in the Cenozoic.

Evidently all but one of the Paleocene specimens of rodents have come from a locality (Bear Creek, Montana) which is unique among Paleocene localities in its lack of any remains of multituberculates (Jepsen, 1949, p. 489). An incisor of a rodent has been reported also from the Clark Fork fauna of the Polecat Bench formation by Van Houten (1944, p. 180). He does not list a directly associated fauna. Multituberculates and rodents have been found in association in the overlying Willwood; so these animals are not always mutually exclusive, at least not during the final appearance of the multituberculates. One such association is mentioned by Van Houten (1944, p. 184).

Seemingly, the evidence of the multituberculates suggests that rodents were rare in the late Paleocene, and either absent over most of the northern hemisphere or present only in isolated areas. It is perhaps possible, if such isolated areas

existed, that each had its own taxonomic group—for example, aplodontoids in one place and muroids in another. But such a distribution suggests a contracting phase in the history of a group, not an early or expanding phase as would be expected at this time. It seems much more likely on the evidence from the Eocene, as well as the actual late Paleocene record, that only primitive rodents (aplodontoids) were then in existence.

Rodents may have had a much greater distribution than is indicated by the known Paleocene record, but if so, could hardly have occupied a wide range of environments. Absence of the rodents from the known late Paleocene of Europe and Asia, and their rarity in North America, supports this conclusion, as well as does the ubiquitous presence of multituberculates. Certainly multituberculates still lived under a wide variety of conditions. The scant record of rodents may be partly the result of environmental restrictions, but the greatly increased numbers present in the early Eocene, essentially of the same kinds and in approximately the same environment, indicates that this is at best no more than part of the explanation. To be specific, only a single incisor of a rodent has been obtained from the latest Paleocene of the Polecat Bench formation. Yet in the same general area, drab beds of similar facies in the overlying Willwood formation yield abundant rodent remains.

Imperfections of the Paleontologic Record

Anyone who has collected mammalian fossils or who is familiar with the increments to faunal lists throughout the years is aware of the danger of drawing conclusions from the reported absence of a group. For example, rodents are unknown in the pre-Oligocene deposits of Asia with the exception of a late Eocene or early Oligocene cricetid (*Cricetodon*) from China. They have not been recorded from the late Eocene Irdin Manha or the latest Eocene Shara Murun beds of Mongolia; nor have they been recorded from the latest Eocene Pondaung of Burma. Nevertheless, it is almost impossible to think that the order was absent from Asia during nearly all of pre-Oligocene time.

Notwithstanding the above, I think the stratigraphic record of the rodents is suggestive of the early history of the order, if taken in conjunction with the multituberculate record and other evidence. At least in North America, where the record of the rodents is longer than elsewhere, once rodents appear they are recorded in every major faunal stage subsequent to the late Paleocene. I have collected from each of these levels, and not only have obtained rodent material from them all, but also some material from each local fauna which I have worked for any time.

Problem of Migration in Paleocene Rodents

Absence of the rodents from the well-known microfaunas of the American middle Paleocene is presumably real. If real, rodents were either not then in existence, or else they were in some area unknown as to fossil content from which they spread into North American centers of deposition in the late Paleocene, but seemingly not into Europe until the early Eocene. That some mammals did migrate into North America in the late Paleocene is suggested also by the first appearance of tillodonts, oxyaenids, and uintatheres in the record. Unfortunately, the outlook for the discovery of either a middle Paleocene rodent or an ancestor of the order thus seems poor. The event is unlikely in North America, and impossible elsewhere until earlier Paleocene beds are discovered.

Two highly speculative considerations suggest that some trace of rodents may yet be found in the middle Paleocene of North America. The rarity of late Paleocene remains is not in accord with the population size seemingly necessary for the extension of range involved in "mi-

gration" over long distances, especially for small animals such as rodents. Neither does a theory of migration agree with a conclusion that might be reached from the evidence; namely, that in the late Paleocene, the rodents had little more than completed an adaptive shift to a truly gnawing mode of life, and were still quite rare. Primary expansion of range probably did not occur until the early Eocene. Further, it must be remembered that rodents are, in fact, unknown as yet from the late Paleocene of either Asia or Europe, but they are known from North America. Although any conclusion would be hazardous, perhaps the actual record is an approximation of the real status of the rodents during the Paleocene.

Summary

A number of lines of evidence have been given which, taken together, suggest a late origin for the Rodentia, or at least a late completion of the adaptive shift which produced the typical structures of the order. It is not possible to fix the duration of this shift, but I think it probable from the available data that it did not begin until the dawn of the Paleocene, and that it ended in or shortly before the late Paleocene. I fail to find in the early history of the placentals any actual evidence to suggest otherwise. None of the data presented in this paper is conclusive in itself, but collectively they are strongly suggestive. The lines of evidence may now be summarized.

(1) The known record from the Eocene indicates: (a) progressive diversification within the Aplodontoidea during Eocene time from one or a few genera, (b) appearance around the Eocene-Oligocene boundary of the modern superfamilies. These data suggest that the early Eocene rodents were near their point of origin in time, and do not support views of a long prior history except as the history might be one of an adaptive shift which produced the typical rodent structures.

(2) The history of the multituberculates suggests the absence or rarity of rodents as competing species during almost all of pre-Eocene time. Not only are rodents rare or absent at this time, but, also, the multituberculates, presumed ecologic predecessors, are widespread and common.

(3) Numerical representation of early Eocene rodents as compared with that of the late Paleocene, under the circumstances prevailing, suggests a group which has just finished a critical phase in its development and is beginning its primary expansion.

(4) Rodents are unknown in the Cretaceous and earlier Paleocene.

(5) Rodents have their first known appearance at a time distinctly later than many other orders of placental mammals. These orders include animals which are also of small or minute size. Further, by middle Paleocene, considerable differentiation has already been achieved within several of these orders. If these orders are of late or latest Cretaceous origin, then the rodents, not reaching a comparable diversity until well within the Eocene, would seem to have originated in the Paleocene.

Summing up evidence for the related question of time of differentiation within the Rodentia, it may be stated that direct evidence from the Eocene supports the thesis that rodents underwent their primary differentiation during the Eocene. Indirect evidence from the pre-Eocene history of mammals supports this proposition in that it suggests a late date for the perfecting of the fundamental structures of the order. Thus, many Paleocene species of placentals and multituberculates possess some kind of rodent-like dentition. Their subsequent disappearance, concomitant with the first known appearance and diversification of the rodents, implies that rodents were, in fact, not varied in the late Paleocene and early Eocene. The rarity of rodents in the Paleocene record (actual but sparse in the late Paleocene of North America; none in the late Paleocene of Europe and

Asia) indicates that the late Paleocene members of the order did not occupy a wide range of environments; if they had, the record would be better than it is. This, to me, suggests lack of differentiation. Finally, the earlier and contemporaneous unguiculates show some differentiation, thus indicating that diversity when present in related groups is recorded (at least partially). Even in quarry assemblages and in some surface concentrations, the large number of unguiculate (and ferungulate) genera and species present, of only small morphologic and taxonomic scope, indicates that the quarry sites or collecting levels are zones drawing samples from various minor ecologic situations. The absence of rodents, or their constancy of type when present, is not, then, the result of peculiar restrictions in environment of the known sediments.

If we attempt to reconstruct the early Cenozoic history of rodents on the basis of what is known or what can be inferred from the historical record (admitting that certain inconsistencies of interpretation and of record exist), we may postulate the following important steps:

(1) Late Cretaceous: rodents were not as yet differentiated from the generalized insectivore stock.

(2) Early and middle Paleocene: unknown pre-rodents emerged and shifted adaptively to a gnawing mode of life. In the absence of objective criteria, it is not possible to say how much of this interval of time is involved.

(3) Late Paleocene: fundamental structures of the order had been acquired. At this time, the rodents were just completing, or had just completed, their adaptive shift. They are still quite rare.

(4) Early Eocene: locally, at least, rodents became abundant in the same areas where they had been rare. It is possible that primary expansion of range occurred at this time.

(5) Middle Eocene: differentiation of the aplodontoid stock. All rodents were still, taxonomically at least, members of the Aplodontoidea.

(6) Late Eocene: development of the modern divisions of the order.

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THE INHERITANCE OF CERTAIN COLOR PATTERNS IN WILD POPULATIONS OF *LEBISTES RETICULATUS* IN TRINIDAD

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INTRODUCTION

Pronounced sexual dimorphism of both form and color is characteristic of a number of viviparous teleost fishes of the subfamily Poeciliinae. The condition is perhaps most pronounced in several small related tropical forms, such as *Micropoecilia branneri* Eigenmann, *Micropoecilia parae* Eigenmann, *Micropoecilia bifurca* Eigenmann, and *Lebistes reticulatus* (Peters), all native to northeastern South America and two to adjacent Caribbean islands, which have been included by Hubbs (1926) in the tribe Poeciliini. Among these small, largely surface-feeding, viviparous top-minnows the females are characteristically of generalized form and of an unspecialized, gray coloration, with very little body marking in the genus *Micropoecilia* and with none whatever in *Lebistes* save the characteristic reticulation. By contrast, the males of these species are brilliantly and characteristically colored and exhibit pronounced and species-specific patterns of courtship and mating behavior. In the genus *Micropoecilia,* the male color patterns within a single species may show decided variation over a wide geographic range, but they are normally quite constant in populations occupying many square miles of territory. Thus, for example, the males of *Micropoecilia parae* show an essentially constant color pattern throughout the very numerous populations which inhabit the lagoons and brackish coastal streams and ditches of the islands of Trinidad and Tobago. It is not known how the male color patterns are inherited in the genus *Micropoecilia.*

In *Lebistes,* as in *Micropoecilia,* the males are small relative to the females, are of pronouncedly different form, and are of brilliant coloration. But the male color patterns, far from being constant within a given population even of restricted scope, are highly variable—so much so that, under natural conditions, it is difficult to find two individuals which exhibit even approximately similar patterns. Indeed, the males of *Lebistes* form one of the most highly polymorphic color series known in nature, in sharp contrast to the monotonous phenotypic uniformity of the females.

The inheritance of male color patterns in *Lebistes* has been studied by Schmidt (1920), by Blacher (1927, 1928), by Kirpichinikow (1935), and more extensively by Winge (1921, 1922a, 1922b, 1927, 1930, 1932, 1934) and Winge and Ditlevsen (1938, 1948), in a long series of interesting investigations. As a result of these it seems clear that in *Lebistes* the male is normally the heterogametic sex and inheritance is typically of the XY pattern. The sex-chromosomes, however, are relatively unspecialized and are not morphologically distinguishable either from one another or from the autosomes. Furthermore, sex determination clearly does not reside entirely with the sex-chromosomes. Normally functional XY females and XX males have been demonstrated by Winge. The haploid chromosome number for the species is 23.

Although the males of *Lebistes* exhibit extreme color polymorphism in their total color patterns, even in restricted wild populations, it is possible to resolve these patterns into a number of components which show clear-cut unifactorial inheritance, together with a number of others

in which the mode of inheritance is not yet evident. As a result of the studies of Winge, Winge and Ditlevsen, Blacher, and Kirpichinikow, the inheritance of more than twenty such pattern elements has been analyzed. A large number of them behave as though sex-linked, either in the Y- or in the X-chromosome. A few appear to be autosomally linked. Nearly all of these elements of color pattern, whatever their linkage, are strictly sex-limited in expression, and appear in the males only at sexual maturity. One or two, such as the pattern *Flavus* recently described by Winge and Ditlevsen (1948), are expressed to a very limited degree in the female, and may appear in the young of both sexes at a comparatively early age.

In addition to these patterns of sex coloration, a number of color factors have been described in *Lebistes* which are clearly unifactorial autosomal recessives and affect the extent of total body pigmentation in both sexes. They include the genes Gold and Blond, described by Haskins and Druzba (1938), Goodrich, Josephson, Trinkaus and Slate (1944), Winge (1948) and Haskins and Haskins (1948), the double recessive Cream (Goodrich, Josephson, Trinkaus and Slate, 1944) and a recessive autosomal factor for albinism (Haskins and Haskins, 1948) non-allelomorphic with the others. These factors do not affect the patterns of secondary sex coloration in the male, except in so far as they may be phenotypically modified through deficiencies of available pigment. In sharp contrast to the sex color-patterns, they are expressed equally in both sexes at maturity, and in the young at birth. None of these recessive mutations for xanthic general body coloration has been described in wild populations in the course of a rather extensive search. It seems probable that they have a very definitely negative selective value under natural conditions. Experimental evidence of this has been obtained by the present authors.

The marked polymorphism of the males of *Lebistes reticulatus* raises many questions of great theoretical interest in studies of the genetics of populations under natural conditions. One of these concerns the proportional distribution of genes for patterns of secondary sex coloration among the X- and Y-chromosomes and the autosomes in response to specific ecological conditions.

Earlier work by the present authors on mechanisms of speciation in *Lebistes* in wild populations in Trinidad (1949, 1950) has indicated that in mating the male sex may be largely responsible for the choice of mate, and that the brilliant male coloration probably functions primarily as a warning factor in intra-sexual competition. Conspicuous color patterns in the male thus may have a positive selectional value in competitive mating—a value probably attaching to the total conspicuousness of the pattern as a unit, rather than to any particular element of it.

It seems quite likely, however, that such conspicuous patterns may have a markedly negative selective value in the presence of predators. There seems little doubt, indeed, that the male *Lebistes* is normally under considerably heavier selectional pressure from predators than is the corresponding female. Data obtained by the present authors, as yet unpublished, have indicated that although the sex ratio in wild populations of *Lebistes* kept artificially under favorable conditions and protected from predators is very close to 1 : 1, the ratio for the same populations in their natural habitat approximates 2 females to 1 male. The results of "release and recapture" experiments in wild populations confirm this greater vulnerability of the male to predation under natural conditions.

The considerably larger size of the mature female of *Lebistes* is no doubt an important contributory factor to its greater average viability. However, at the time of sexual differentiation, when the color patterns of the male first appear, the young male and female are of closely comparable size. If size were the

only advantage possessed by the female, it would be expected that females would be decimated quite as rapidly as males during this period of early maturity. It seems highly probable that the conspicuous color patterns of the male are an important contributory factor in its vulnerability to predators, particularly in clear and shallow stream waters, where *Lebistes* frequently occurs.

It is well known from the studies of Winge and his co-workers that crossing-over between the X- and the Y-chromosomes occurs rather readily in *Lebistes*. It is not improbable that similar crossing-over may occur in the autosomes.

If the foregoing premises are correct, it seems likely that brightness of pattern in the male of *Lebistes* is normally subject to cross-selectional forces in wild populations, and it seems possible that the relative magnitude of these forces may influence the frequency of distribution of the genes for sex-coloration between the Y-chromosome on the one hand and the X-chromosome and the autosomes on the other.

In a population well protected from predation, for example, natural selection might well favor the development of intense color patterns, on the one hand, and on the other might favor the accumulation of genes for such patterns in the Y-chromosome. For any mutation contributing to the positively selected brightness of pattern which was Y-linked would be transmitted to all the male progeny of any mating, irrespective of the female parent, and would thus become phenotypically established in the population by the most efficient path.

Where predation is especially heavy, it is possible that selection in the reverse direction may take place, toward less intense pigmentation of the males on the one hand and toward an accumulation of color genes in the X-chromosome and the autosomes on the other. For X-linked and autosomally linked factors will have a permanently "protected" reservoir available in the female population, in which, whether they are present in heterozygous or homozygous condition, they are sex-limited and will not be phenotypically expressed.

A comparative study of the distribution of genes for secondary sex coloration in *Lebistes* in various wild populations therefore seems of considerable interest. Such a study has been begun. The experiments reported herewith are preliminary in character. They were designed only to explore the general pattern in certain wild populations. Nevertheless, they seem of sufficient interest to report at this time, primarily because they offer some answer to the oft-raised inquiry as to whether the inheritance of secondary sex color patterns in wild populations of *Lebistes* is predominantly or exclusively Y-linked, as has been suspected at various times.

Geographic Situation

The Northern Range of the Island of Trinidad offers a remarkably convenient and versatile physiographic situation for population studies of *Lebistes*. Extending along essentially the whole northern margin of the island, this mountain chain is a prolongation as a series of parallel ridges of the coastal cordillera of Venezuela. The average elevation of the main ridge is about 2,000 feet, rising in the vicinity of the peaks of El Tucuche and El Aripo to well over 3,000 feet. The northern slopes are dissected by a series of short roughly parallel streams emptying individually into the sea, with no freshwater connections between them. Since *Lebistes* in Trinidad apparently occurs rarely if ever in the open marine littoral (we have never found individuals in such situations), it is probable that the populations of these streams are almost if not completely isolated from one another. By contrast, seven considerable streams which flow southward in approximately parallel courses along the landward drainage of the Northern Range are tributaries of a single major westward-flowing river, the Caroni, which drains into the Caroni Swamp, near Port of Spain. The upper

courses of these streams are well-defined and often precipitous, and are probably never connected by flood water. The lower courses, near their points of confluence with the main river, on the other hand, are low and swampy and subject to extensive flooding during the rainy seasons. *Lebistes* have been found at all points along this drainage system, except in the extreme upper courses of the parallel streams or their smaller tributaries. Westward and eastward of the Caroni drainage system other southward-trending streams, like those of the northern drainage, flow in approximately parallel courses to the sea. Thus it is possible, in this geographic situation, to deal on the one hand with populations of *Lebistes* which must constitute almost or completely physiographically isolated breeding units. On the other, in the Caroni drainage, populations of different streams are connected by continuous series of forms, and isolation between them, if it exists, must be due to biological rather than physiographic factors.

Lebistes is most abundant in those portions of the Caroni drainage where the water volume is rather low and the streams are only moderately swift. They occur in particular abundance in relatively shallow, broad, clear pools with gravelly bottoms subject to active but not excessive currents and provided with fair cover in the form of pebbly debris. Most of the populations used in the present study were obtained in such locations. The number of predators present varied greatly with the location, and also with the season. Various characins and cichlids (especially *Aequidens latifrons*) were abundant and probably quite destructive in certain locations, much less so in others. Predation from fishing birds is probably somewhat less severe, despite the relative conspicuousness of the *Lebistes* males, which often flash conspicuously to a human observer situated as much as twenty feet above the water.

Since it was planned to concentrate the general study in this geographic area, material for the present studies was drawn from this part of the island. Samples were taken from one of the northward-flowing streams, the Marianito, which originates near the highest point of the Range, from the Maraval, a southward-flowing stream which empties into the Gulf of Paria westward of the Caroni Swamp, and from the Maracas, St. Joseph, and Arima Rivers, all parallel south-slope streams connected through the Caroni system, as well as from one or two unspecified points in the Northern Range.

Material and Methods

Wild cultures collected from these locations were brought to a laboratory greenhouse especially designed for the breeding of viviparous poeciliids and containing between four and five hundred tanks. Wild males were used in crosses with laboratory stock shortly after capture, or, in a few cases, were used after having been maintained for a few months in stock cultures. Young fish from wild cultures were individually isolated, and the virgin females so obtained were used in crosses with males of domestic stock.

At maturity, all males from these crosses were killed and immediately photographed in color at approximately natural size with a Leica camera on 35 mm. Kodachrome film. Transparencies so made were filed in a manner to permit their ready detailed comparison, by superposition or against a white background. Especially interesting series were dehydrated in absolute alcohol and mounted in xylene, a procedure which retains most of the elements of the color pattern with satisfactory fidelity.

Laboratory stocks containing five known factors for sex coloration were used in the crosses with the Trinidad material. All of them were obtained through the kindness of Dr. Winge from his laboratory in 1934 and have been maintained in pure culture since that time. The first of these, *Maculatus*, was described by Winge in 1922. It is manifested in the

adult male as an intense melanic spot in the dorsal fin, combined with characteristic red lateral body markings. The second and third, *Armatus* and *Pauper*, were obtained by Winge in 1922, the former from Danish domestic stock, the latter from the West Indies, and were described in 1927. They lead respectively to the elongation and coloration of the lower rays of the caudal fin, producing a "swordlike" effect, and to the formation of characteristic red and blue color-patterns about the tail. All three of these characters have been found by Winge (1948) to be "absolutely" Y-linked and probably allelomorphic. They are therefore normally absent from the gene-complex of the female. The remaining two characters used, *Coccineus* and *Vitellinus*, were described by Winge in 1927, and lead to specific color patterns in the caudal region. Both behave as though located in both the X- and Y-chromosome, and show a fairly high crossover percentage. Both are dominants, as shown by Winge (1927) in the case of sex-reversed females heterozygous for both characters, in which they were phenotypically exhibited. The probable allelomorphs *Ma*, *Pa*, and *Ar*, since they are represented only in the Y-chromosome, cannot be considered as typical dominants, but are always phenotypically expressed. Thus the situation for these color-factors, at least, resembles that in the polymorphic grouse locusts of the genera *Apottetix* and *Paratettix* and in certain land-snails of the genus *Helix* in that the uncolored condition of the female may be regarded as a common "universal recessive"—a condition pointed out by Haldane (1930) and Ford (1945). It is to be noticed, however, that no uncolored males have been reported in *Lebistes*—indeed, there is reason to believe that such uncolored forms would be at a pronounced selectional disadvantage.

The Analysis

If a wild male of unknown genetic constitution be crossed with a female of $X_0X_0A_0A_0$ constitution (where the analysis refers only to genes for secondary sex-color patterns and A_0A_0 is taken to indicate the constitution of all the autosomes in this respect) it is to be expected that those portions of the color pattern which are controlled by genes located in the X-chromosome will be absent in the F_1 male progeny, but present in heterozygous form in their female siblings. If it appears in all F_1 male progeny, on the other hand, it is either Y-linked or was homozygous in an autosome of the original male. If the character appears in ½ of the F_1 male progeny, it follows that it was autosomally linked, and present in the heterozygous condition, in the original male. In alternatives (1) and (3), the data secured can be made of essentially unequivocal significance. In alternative (2) a distinction can be made between Y-linked and autosomal factors either by backcrossing the F_1 male to a female of $X_0X_0A_0A_0$ composition, or, alternatively, by crossing the F_1 female to a male of composition $X_0Y_QA_0A_0$, where Q represents a known Y-linked color factor. (It would be unnecessary to introduce Q if colorless males of *Lebistes* were known.) In such case, if the unknown factor appears in ½ of the male progeny of this cross, it may be supposed to have been located in the autosome. If it is not present in the male progeny, it has behaved as though Y-linked. In such an analysis, it is of course necessary to select Q in such a way that as large a portion of the male as possible be uncolored, to permit maximum expression of the phenotype which is being sought. This condition is well fulfilled by the races *Maculatus*, *Armatus*, and *Pauper* already described. This was the method of analysis through which the data reported in Table I were obtained.

If a wild female of unknown genetic constitution be crossed with a male of constitution $X_0Y_QA_0A_0$, the F_1 male progeny may be of the race of the male parent or may show additional color patterns. In the former case, the indication

is relatively unequivocal that no expressible color factors were carried by the female. If additional patterns appear in all of the F_1 male progeny, the genes determining such patterns were obviously linked either to the X-chromosomes or to the autosomes and were homozygous in the original female, while if one-half of the F_1 males show the additional pattern, such genes were present in heterozygous condition. A further distinction between autosomally linked and X-linked genes can be made by backcrossing the F_1 males to females of composition

TABLE I. *Preliminary analysis of wild males*

Series no.	Cross no.	Collection locality	Stock and sex of laboratory parent	Number and description of male progeny	Indicated linkage of patterns observed
1	13	Maraval River	Female, Ma Stock. ($X_0X_0A_0A_0$)	Five, all like parent in body pattern but elements of caudal pattern uniformly absent.	Caudal elements X-linked. Remaining pattern either Y-linked or autosomal.
2	14	Caroni Drainage	Female, Ma, Co, Vi Stock. ($X_0X_{Co,\,Vi}A_0A_0$)	Eight, all duplicating full parental pattern. Co, Vi superposed in ½ of brood.	No X-linked elements. All elements Y-linked or autosomally linked.
	14a	Female, FI of above	Male, Ma Stock. ($X_0Y_{Ma}A_0A_0$)	Three, all Ma, Co, Vi. No elements of wild pattern.	
3	25	St. Joseph River	Female, Pa Stock. ($X_0X_0A_0A_0$)	Ten, all duplicating full parental pattern	All elements Y-linked.
	25a	Female, FI of above	Male, Pa Stock. ($X_0Y_{Pa}A_0A_0$)	Ten, all Pa. No elements of wild pattern.	
4	26	St. Joseph River	Female, Ar Stock. ($X_0X_0A_0A_0$)	Eight, all duplicating dorsal pattern of parent, all lacking parental caudal pattern.	Caudal elements probably autosomal and heterozygous.
	26a	Female, FI of above	Male, Pa Stock.	Seven, all duplicating dorsal, pattern of wild male, all lacking caudal pattern of wild male.	Dorsal elements autosomally linked, or both X and Y linked.
5	27	Trinidad, precise location unknown	Female, Pa Stock. ($X_0X_0A_0A_0$)	Eight, all duplicating parental caudal pattern.	Caudal elements autosomally linked.
	27a	Trinidad, precise location unknown	Male, Pa Stock. ($X_0Y_{Pa}A_0A_0$)	Twenty, all duplicating wild caudal pattern.	
6	28	Trinidad, precise location unknown	Female, Pa Stock. ($X_0X_0A_0A_0$)	Twelve, all duplicating parental pattern, though with somewhat variable caudal pattern.	No X-linked elements. All elements Y-linked or autosomally linked.
	28a	Female, FI of above	Male, Ma Stock. ($X_0Y_{Ma}A_0A_0$)	Three Ma, lacking wild pattern.	

TABLE I.—*Continued*

Series no.	Cross no.	Collection locality	Stock and sex of laboratory parent	Number and description of male progeny	Indicated linkage of patterns observed
7	29	St. Joseph River	Female, Pa Stock.	Fourteen, all duplicating all elements of parental pattern.	Elements predominantly Y-linked. Possibly some autosomally linked elements (or modifiers).
	29a	Female, FI of above	Male, Pa Stock. ($X_0Y_{Pa}A_0A_0$)	Five, typical Pa except for faint caudal marking.	
8	32	St. Joseph River	Female, Ar Stock. ($X_0X_0A_0A_0$)	Twenty-three, all duplicating parental pattern.	No X-linked elements. All elements Y-linked or autosomally linked.
	32a	Female, FI of above	Male, Pa Stock. ($X_0Y_{Pa}A_0A_0$)	Three, typical Pa.	
9	42	Maraval River	Female, Ma Stock. ($X_0X_0A_0A_0$)	Eight, all duplicating all elements of parental pattern.	Body elements of pattern Y-linked or autosomally linked. Caudal elements autosomally linked.
	42a	Female, FI of above	Male, Ma Stock. ($X_0Y_{Ma}A_0A_0$)	Three, all Ma but one showing caudal pattern of wild male.	
10	45	Marianito River	Female, Ma Stock. ($X_0X_0A_0A_0$)	Eight, duplicating parental body pattern, but with loss of caudal spot in caudal pattern.	Body elements of pattern Y-linked or autosomally linked. Caudal elements both X-linked and autosomally linked.
	45a	Female, FI of above	Male, Ma Stock. ($X_0Y_{Ma}A_0A_0$)	One, Ma, but with caudal pattern of wild male.	
11	50	Santa Cruz River	Female, Ar Stock. ($X_0X_0A_0A_0$)	Fourteen, all duplicating parental pattern.	All pattern elements Y-linked or autosomally linked. No elements X-linked.

$X_0X_0A_0A_0$. Data obtained from the first portion of this analysis are shown in Table II. The analyses of both Table I and Table II are based on the assumption that the genes for unanalyzed sex color patterns in wild populations, like those analyzed by Winge and others, behave phenotypically as dominants, at least when they affect a portion of the body surface not already pigmented. They are also based on the assumption that both wild and laboratory-stock females were of X_0X_0 composition. Although females of XY composition are known to occur, they can be detected through the abnormal sex ratios to which they give rise in the F_1 progeny. It is quite possible that the penetrance of certain patterns is decidedly affected by unknown modifiers. This, of course, could not be accounted for in the analysis, and it may have been involved in certain situations, like No. 26, which

TABLE II. *Preliminary analysis of wild females*

Series no.	Cross no.	Collection locality	Stock and sex of laboratory parent	Number and description of male progeny	Indicated linkage of patterns observed
1	5	Marianito River	Male, Ar Stock. ($X_0Y_{Ar}A_0A_0$)	Sixteen, all typical pattern of Ar stock.	No expressed X-linked or autosomally linked patterns.
2	6	Arima River	Male, Ma Stock. ($X_0Y_{Ma}A_0A_0$)	Five, all typical Ma, but with added caudal pattern.	Caudal elements X-linked or autosomally linked.
3	9	Arima River	Male, Pa, Co, Vi Stock. ($X_{CoVi}Y_{Pa}A_0A_0$)	Eight, all typical Pa, but with added caudal pattern.	Caudal elements X-linked or autosomally linked.
4	22	Arima River	Male, Ma, Co, Vi, Stock. ($X_{CoVi}Y_{Ma}A_0A_0$)	Four, all typical Ma-CoVi, without additional pattern.	No expressed X-linked or autosomally linked patterns.
5	38	Marianito River	Male, Ma Stock.	Five, all typical Ma without additional pattern.	No expressed X-linked or autosomally linked patterns.

yield puzzling results under conventional examination. Much more extensive analyses are required. However, these preliminary results do give decided indication as to whether or not this type of inheritance in wild populations takes place primarily through the Y-chromosome—its principal purpose.

The data in table III were obtained through the use of certain laboratory stocks which had been made up to test the rate of diffusion of genes in stream populations, using the character *Maculatus* as a marker. These stocks were derived from the F_1 hybrids of females from various wild populations with males of *Maculatus* laboratory stocks. The males of these F_1 hybrids were then twice backcrossed to females of the same wild stock, and the resulting progeny propagated for several generations. The resulting population was thus, on average, of seven-eighths wild genetic constitution. Any color patterns beyond that of *Ma* detected in the males must have been introduced as X-linked or autosomal factors by one of the three wild females with which crosses had been made, thus giving a measure, again, of the presence of such genes in the wild populations.

TABLE III. *Analysis of wild stocks twice backcrossed to Maculatus*

Location of original female	Number of progeny showing only typical Maculatus pattern	Number of progeny showing additional factors (all caudal patterns)
Marianito River	9	64
Maracas River	21	0
St. Joseph River	72	6
Arima River	3	3

DISCUSSION

The data reported herewith, as already stated, were designed only to ascertain, in a very general way, whether X-linked and autosomally linked color patterns occur in wild populations of *Lebistes* in frequencies comparable to those of Y-linked factors. The summary of this data in Table IV indicates that this indeed is true.

The preliminary analyses were not carried sufficiently far to distinguish between classes of linkage in many instances, nor are the recorded broods sufficiently large to determine, in many cases, whether X-linked or autosomal factors were present

TABLE IV. *Summary of distribution of linkages of pattern genes from table I and table II*

	No. Y-linked	No. X-linked	No. autosomal	No. Y-linked or autosomal	No. X-linked or autosomal
Table I (Wild Males)	2 (1)*	2 (1)*	(2)* 3	7	
Table II (Wild Females)					2

* Alternative interpretation from No. 26.

in the homozygous or the heterozygous condition. It is evident, however, that factors for color patterns in *Lebistes* which behave as though located in the X-chromosome or in the autosomes are by no means rare in wild populations in these Trinidad locations.

The data emphasize the extraordinary flexibility of color polymorphism in wild populations of *Lebistes* and suggest how sensitive it may be to factors of selection. It seems clear that the total color pattern of a mature male may, on the one hand, be inherited in a strikingly unitary fashion and may depend upon a single gene or a series of genes which are relatively tightly linked.[1] This unity of rather complex patterns certainly obtains in the laboratory stocks Pa, Ar, and Ma, and it seemed to do so in several of the males examined (nos. 29 and 42 of table I, for example). Such patterns may be of unusual brilliance and great complexity, and although they show some phenotypic variability in F_1 male progeny, this is surprisingly small. On the other hand, male patterns may be highly composite and made up of a large number of elements, the genes for which may be distributed among the X- and Y-chromosomes and the autosomes. In such cases, the situation seems almost certainly to be typical of polygenic characters in general—mutually reinforcing characters, often almost identical in phenotypic effect but referable to differing genes often located in different chromosomes, are common.

[1] It is quite possible that comparatively large linked sectors of chromosomes, or even whole linked chromosomes are involved here—a condition characteristic of the grouse-locusts and *Helix*, as Haldane (1930) has pointed out.

In such a situation, much more extensive comparative analyses of wild populations existing under differing natural conditions seem well worth while, and these have been undertaken.

SUMMARY

A preliminary analysis is presented of the mode of inheritance of patterns of male secondary sex coloration in several wild populations of *Lebistes reticulatus* in Trinidad. A high proportion of such factors were found to behave as though Y-linked in inheritance, but a substantial number behaved as though located in the X-chromosome or the autosomes. In some cases complex and brilliant patterns were found to behave as though under the control of a single gene, or of a series of very tightly linked genes. In others, patterns were obviously composite and under the control of several genes.

It seems likely that this situation of polymorphism will be found to be highly sensitive to selectional factors. There is some indication that two of the most important of these may involve the advantage in competitive mating secured through brilliant male patterning as a positive element and the greater vulnerability to predation of conspicuously colored males as a negative one. Both of these factors may be expected to be proportional to the total conspicuousness of the coloration but largely independent of specific patterns. Thus it might be supposed that a wide distribution of individual patterns would characterize a single population. This appears to be true of *Lebistes* in Trinidad. It might be further supposed that X-linked or autosomal patterns would

tend to be emphasized in populations existing in environments characterized by heavy predation, because of the reservoir for such factors available in the uncolored females. By the same token, it might be expected that Y-linked factors would predominate in populations of *Lebistes* which had long been protected from predators. Further analysis of such situations is planned.

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MATING OF EBONY VESTIGIAL AND WILD TYPE *DROSOPHILA MELANOGASTER* IN LIGHT AND DARK

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Introduction

Many observers have shown that there are sufficient differences in mating behavior between most species of *Drosophila* to prevent transspecific matings under natural conditions or at least to reduce them to an extreme rarity (Dobzhansky, Mayr, Spieth, Stalker, Wallace and others). In most cases it is the female that refuses to take part in the courtship, the male being prepared to court with almost anything. That this is not always the case has been shown by Miller (1950) who observed that males of the species *Drosophila affinis* and *Drosophila algonquin* courted females of the same species more readily and more persistently than those of the other.

Some studies have been made of differences in mating behavior between members of the same species. In recent years Mather and Harrison (1949) have demonstrated mating preferences between highly selected lines of *D. melanogaster;* Rendel (1945) showed that in *Drosophila subobscura* yellow males are distasteful to females that are not yellow, though yellow females mated normally. Merrell (1949) showed that yellow males in *D. melanogaster* appeared to behave similarly to yellow males in *D. subobscura,* and that cut females were not readily mated by any sort of male. It is not always possible in the earlier work to distinguish between a specific mating preference and an indirect effect of general vigor. For example, in competition with normal males, yellow-white males, because of their inferior all-round vitality, would inseminate relatively few females no matter what the females were.

Studies of mating behavior are of interest in three ways: they demonstrate the extent to which separations of species can be brought about by mating preferences; they show to what extent mating is at random in populations; and they allow one to measure approximately the extent to which different mating behaviors contribute to the fitness of the genotypes determining them. This paper describes the result of matings using males from ebony, vestigial and wild type stocks under different illuminations. It shows that the mating behavior of homozygous males depends on whether matings are carried out in the light or the dark, and that this affects their fitness. The investigation arose out of an attempt to discover if the presence of light facilitated mating in *Drosophila melanogaster.* In *Drosophila subobscura* light is necessary for mating to take place (Rendel, 1945). Although in other species, including *Drosophila melanogaster,* light is not necessary, it was thought possible that light might nevertheless have some effect if tests of sufficient discrimination could be carried out. During trials of this sort using flies from ebony, vestigial, and wild type stocks, the first observations were made which led to the more detailed investigation described here. It should be noted here that differences ascribed to the genes ebony and vestigial may be due to other genes in the stocks used although stocks are identified here according to the presence of ebony or vestigial.

Description of Experiment

As the state of nutrition of *Drosophila* makes a considerable difference to mating behavior, all flies used in comparisons in the following experiments were taken

from the same bottles. Fertilized ebony and vestigial females were put into bottles without males in proportions which would lead to approximately the same number of flies of the two types emerging in the next generation. Mating tests were carried out on flies emerging from these bottles on the same day. Two sorts of tests were made. In the first, males and females which had been aged separately for three days were mated for one and a half to two hours and the females were dissected to determine whether they were inseminated or not. Only one type of male was used in each vial in this sort of experiment, though in most the males were mated to a mixture of ebony and vestigial females. In the second series of experiments, either vestigial or ebony females were mated to a mixture of two sorts of males for 24 hours, after which the females were put in single female cultures so that one could determine whether they were inseminated by a vestigial or an ebony male. In all experiments the number of flies to be mated in the light was exactly balanced against those to be mated in the dark, but owing to losses through death during aging, and escapes during transference from vial to vial, the numbers finally examined were not always exactly equal. All matings were made without etherizing in a constant temperature room at 25° C. Flies mated in the dark were put into tubes of black photographic paper sealed at both ends.

Results

The first set of experiments are summarized in table 1, and compare the effect

TABLE 1. *Comparison of results of mating vestigial or ebony males with both types of female in light and in dark*

		Light							Dark						
			Females							Females					
		No. males	e		vg		Total		No. males	e		vg		Total	
			+	−	+	−	+	−		+	−	+	−	+	−
Vestigial Males		15					1	9	14					4	7
		40	7	15	10	17	17	32	42	12	17	16	14	28	31
		25	6	3	13	2	19	5	25	5	3	16	4	21	7
		20	1	19	7	13	8	32	20	1	19	3	17	4	36
		10	10	1	7	3	17	4	5	4	0	4	1	8	1
		30	13	2	11	4	24	6	20	7	2	5	4	12	6
	Total	140	37	40	48	39	86	88	126	29	41	44	40	77	88
	Successful Matings						49.4%							46.6%	
Ebony Males		21					0	19	12					8	0
		65	2	35	1	28	3	63	68	16	18	9	19	25	37
		7	0	2	0	4	0	6	8	2	0	4	0	6	0
		35	9	22	7	23	16	45	35	21	11	12	16	33	27
		40	16	6	4	22	17	50	30	30	5	11	4	41	9
	Total	168	27	72	14	59	41	150	173	69	34	36	39	113	73
	Successful Matings						21.5%							60.7%	

"+" indicates an inseminated female; "−" one that is not inseminated.

TABLE 2. *Matings between a mixture of ebony and vestigial males and either vestigial or ebony females*

Expt. no.	Light						Dark					
	No. of e ♀ ♀ inseminated by—			No. of vg ♀ ♀ inseminated by—			No. of e ♀ ♀ inseminated by—			No. of vg ♀ ♀ inseminated by—		
	e ♂	vg ♂	Both	e ♂	vg ♂	Both	e ♂	vg ♂	Both	e ♂	vg ♂	Both
A	7	36	—	8	24	—	14	23	2	20	15	—
B	7	23	—	10	16	1	9	18	1	12	14	5
C	3	16	—	6	17	—	10	12	6	34	8	1
D	6	26	—	15	35	—	11	12	7	11	6	—
Totals	23	101	—	39	92	1	44	65	16	77	43	6
Total ebony matings				62.5						132		
Total vestigial matings				193.5						119		

of mating ebony males or vestigial males for 1½ to 2 hours in the light and in the dark. The proportion of females inseminated by vestigial males in the light is a little higher than the proportion inseminated in the dark but not very markedly so. In contrast ebony males inseminate a far higher proportion of females in the dark than they do in the light, 60.7% being inseminated in the dark and only 21.5% in the light. There was no obvious difference between the two types of females used in the likelihood of their being mated, both standing about an equal chance of being inseminated by either sorts of male in light and dark. It may be noted that though vestigial males are overall slightly more successful than ebony males and twice as successful in the light, they are much less successful in the dark.

As comparisons of males cannot be made satisfactorily, only on the evidence provided by the first sort of experiment, ebony and vestigial males were allowed to compete with each other in the same vial. The females used were either all ebony or all vestigial and were aged for three days before mating. The results are set out in table 2. In experiments A and B of this series, males were not aged before mating. In experiment C they were aged one day and in experiment D they were aged 3 days. In experiment A flies mated in the light were exposed to a normal night interval of darkness. In the other three experiments all those mated in the light were in the light for the whole mating period. Mating took place for 24 hours in all experiments.

Aging the males before mating does not seem to have made any difference in the results of mating carried out in the light, but in the dark there is an obvious increase in the success of ebony males with increase in age. Adding together experiments A and B, and scoring mixed matings as one-half to each type of male, we find that in the dark there were 59 ebony matings to 74 vestigial ones, but adding together experiments C and D we find 73 ebony matings to 45 vestigial ones. Males of different ages were used because it was suspected that ebony matured more slowly than vestigial. Although vestigial flies take a day longer to develop from egg to imago, virgin vestigial females emerging on the same day as ebony will lay eggs nearly a day earlier. The suspicion that vestigial males might have a similar initial advantage over ebony is borne out by this experiment.

Turning to the comparison between ebony and vestigial males in the light, we find that vestigial males were far more successful, mating 193½ times as compared to 62½ times by ebony males. In the dark on the contrary vestigial mated only 119 times to ebony's 132. Considering only the effect of the two genes on

TABLE 3

	Light				Dark			
	ebony ♀♀		vestigial ♀♀		ebony ♀♀		vestigial ♀♀	
	e ♂	v ♂	e ♂	v ♂	e ♂	v ♂	e ♂	v ♂
Exp.	30.27	93.73	32.23	99.77	65.74	59.26	66.26	59.74
Found	23	101	39.5	92.5	52	73	80	46
	+7.27	−7.27	−7.27	+7.27	+13.74	−13.74	−13.74	+13.74

mating behavior in the male and giving vestigial a fitness of one, this means that in the light, the ebony male has a fitness of 0.48 whereas in the dark it has a fitness of 1.05.

The proportion of the two types of females inseminated by one or the other type of male is not distributed according to the proportion of all females inseminated by that type of male. Table 3 shows what one would expect against what was actually found. In every case there is a tendency for unlike to mate with unlike. The apparent contradiction between this result and that of the first series of experiments is false. The apparent tendency of like to mate with like shown in the totals of table 1 is present in three trials out of five, the tendency in the other two being the reverse. Most of the preponderance of matings of like by like in the totals is due to the fact that more vestigial flies were used in the most successful trials. In any event in Experiment One the competition is not between two types of male but between two types of female for the same type of male.

A final point worth noting in these experiments is the occurrence of double matings. They are far more frequent in the dark than in the light and also more frequent with ebony than vestigial females. Normally a female refuses a second mating immediately after copulation. It is not clear what the more frequent occurrence of double matings in the dark signifies. It would be interesting to know how soon after mating females normally accept a second mating and whether the time interval is much affected by light or dark.

The small amount of data available on the mating of wild type males in light and dark is set out in table 4 together with the results of some matings of e × e and vg × vg. The time of exposure was two hours. They are in agreement with previous results in showing that ebony males mate more successfully in the dark than in the light, whereas vestigial males are more successful in the light. They also show that wild type males like vestigial males are more successful in the light.

Although experiments discussed in this paper were made on ebony and vestigial flies from different stocks and may therefore have differed in other ways, it can be shown that the main effect is closely associated with the ebony gene. Ebony and vestigial flies were crossed and kept heterozygous for 10 generations after which ebony, vestigial and wild-type stocks were re-extracted. Table 5 shows that whereas vestigial and wild type males mate equally in light and dark, ebony is more successful in the dark.

TABLE 4

Mating	Light		Dark	
	+	−	+	−
e × e	5	36	24	19
vg × vg	18	27	7	39
+ × +	38	29	16	42

TABLE 5

Males	Light ♀♀		Dark ♀♀	
	+	−	+	−
Vestigial	18	15	23	12
Ebony	25	69	65	18
++	29	1	30	0

Conclusions

Owing to the many environmental influences on mating behavior it is difficult to give a detailed interpretation of the results presented here. In the author's opinion, only clear-cut major effects are reliable. One factor which tends to make results uneven, and which could be overcome only by the laborious method of doing paired matings, is that one successful courtship stimulates other males in the same tube to redoubled activity. When mating has been allowed to take place over 24 hours, as in the second set of experiments, the probability of this factor influencing one vial more than another is less than it is when mating is restricted to an hour or so.

It seems safe to draw the following conclusions from the experiments reported here. Disturbances of mating of a major kind can be brought about by gene changes, and these disturbances can give rise to drastic reductions in the fitness of affected animals. In these experiments the gene ebony reduces the fitness of homozygous males, through mating failure alone, to 0.48 in competition with vestigial males if the fitness of the latter is taken as 1, and if mating is in the light. It is even more striking that in a different environment, namely in darkness, homozygous ebony males become fitter than vestigial males, the relative fitness of ebony males in the dark being 1.05.

Ebony and vestigial males both mate preferentially with females of the type not their own, and vestigial males are more successful in competition with ebony males when both are young. The mechanism causing these phenomena is not understood. The fact that vestigial and wild-type males both mate more readily in the light than in the dark is believed to be a result of increased general activity in the light.

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NATURAL SELECTION IN *DROSOPHILA MELANOGASTER* UNDER LABORATORY CONDITIONS [1]

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INTRODUCTION

The experiment here reported is an investigation into the effect of natural selection and genetic drift upon the frequency of four sex-linked genes either alone or in all possible combinations in highly uniform continuous populations of *D. melanogaster*. Small continuous laboratory populations were maintained by the population bottle technique of Reed and Reed (1949) which is comparable, on a smaller scale, with the population cage of L'Heritier and Teissier (1933), Wright and Dobzhansky (1946). A related aspect of this problem was investigated by Merrell (1949) who studied "Selective Mating in *D. melanogaster*" in the same stock. The effects of mutation, mutation pressure, and migration—important factors in evolution (Wright, 1931)—are not considered, since their effects in this experiment are believed to be so small, in relation to the factors studied, as to be unimportant.

MATERIALS

Four sex-linked genes were used in this experiment. They determine the following characters: yellow body color (*y*) located at 0.0; cut wings (*ct*^{6}) at locus 20.0; raspberry eye color (*ras*^{2}) at 32.8; and forked bristles (*f*) at 56.7. These four genes cover 56.7 units of a total map distance of 70 units (Bridges and Brehme, 1944).

The stock used in these experiments was developed by inbreeding Lausanne-Special (L-S) stock which is wild type, brother by sister, for thirty generations. A *yct*^{6}*ras*^{2}*f* stock was crossed to the L-S stock every other generation (to the offspring of the single L-S pair giving rise to the generation) with the result that soon all autosomes of the two stocks were identical and any changes in the L-S stock that occurred during inbreeding would be incorporated into the *yct*^{6}*ras*^{2}*f* stock at the same time. The *yct*^{6}*ras*^{2}*f* chromosome probably retained its original composition to a considerable extent, though the individual genes and combinations of two or three genes had some of the L-S X chromosome incorporated. Merrell (1949) has given a detailed account of the procedure.

Homozygosity was not reached by the above breeding plan since seven of the fifteen culture series studied contained small numbers of sepia (eye color) flies. This gene was inadvertently introduced into the inbred stock during the process of inbreeding. Sepia flies were present in small proportions, usually a fraction of 1% and were included with wild type. The heredity of the flies used can be said to have been closely controlled.

Fifteen different substocks each homozygous for one, two, three, or all four of the mutant genes were extracted by selecting males of the desired genotypes and mating each of them separately to virgin L-S females of the inbred line. The heterozygous daughters were then bred back to their father or a male of the same genotype to obtain the homozygous recessive flies of each substock.

The following substocks were thus extracted:

1. *y+++*	6. *y+ras+*	11. *yctras+*
2. *+ct++*	7. *y++f*	12. *y+rasf*
3. *++ras+*	8. *+ctras+*	13. *yct+f*
4. *+++f*	9. *+ct+f*	14. *+ctrasf*
5. *yct++*	10. *++rasf*	15. *yctrasf*

[1] Adapted from a thesis presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University.

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Methods

The population bottle technique developed by Reed and Reed (1949) enables the continuous maintenance of small populations of *Drosophila*. The method consists of so joining two milk bottles, each containing medium, that adult flies can readily pass from one to the other without danger of escaping. Each of the two bottles is alternately and periodically replaced with a new bottle containing fresh medium. A modification of the original method, used in these experiments, consisted of the use of a three inch collar made of automobile radiator hose to join the two bottles conveniently and tightly. Each collar had a single half-inch diameter hole punched out, which was plugged with cotton, to provide for gaseous exchange.

Long maintained cultures of *Drosophila* frequently develop mite infestations. To control mites, so far as possible, pieces of double thickness paper toweling were soaked in a 10% solution of benzyl benzoate (in 95% ethyl alcohol). One such piece of treated paper toweling was placed in each culture bottle before use.

The method of sampling the population of each culture was as follows: The bottles were stood on end, the more recently added bottle uppermost. A 50-watt frosted light bulb was suspended a few centimeters above the base of the upper bottle. After five to ten minutes the upper bottle was removed from the collar and the contained adults etherized and examined. During this time the old medium bottle, plus the collar, was inverted in a petri dish with the open collar as a base. Meanwhile the mouth of the newer bottle was covered by a paper milk bottle cap. Removal of flies from the fresh culture bottle ensured flies free from soft food and debris. It is estimated that the sample of each culture consisted of from 25% to 100% of the adult flies present. Practically all living flies were examined in cultures in which few adults were present while the sample taken from densely populated cultures consisted of a smaller proportion of the total population but was much greater in actual number.

Each culture bottle started throughout these experiments contained an initial population of twenty-five flies, of which twenty were male. Since all fifteen possible combinations were studied, the chromosome concerned might bear from one to four mutant genes. Ten males of this initial population were of the inbred L-S stock; the other ten males of the initial population carried the mutant gene/or linked mutant genes; the five virgin females were heterozygous for the mutant gene/or linked mutant genes. For example, each of the thirteen cultures of the $++ras+$ culture series had an initial population of ten L-S males (wild type), ten $++ras+$ males, and five virgin heterozygous females $\left(\frac{++ras+}{++++}\right)$. Similarly each of the fourteen cultures of the $+ctrasf$ culture series had an initial population of ten L-S males (wild type), ten $+ctrasf$ males and five virgin heterozygous females $\left(\frac{+ctrasf}{++++}\right)$.

The above composition for an initial population was chosen because selection for or against a given gene or linked gene combination would be easily detectable for the following reasons: (1) a population of the indicated composition is theoretically in equilibrium for a sex-linked gene if mating is random and there is no differential selection or genetic drift, (Robbins, 1918); (2) a gene frequency of 0.5 is quickly amenable to the effects of selection. Wright (1931) points out that change in the frequency of a given gene (q) is most readily accomplished when the gene frequency is somewhere near the middle of its possible range, and is least when q is near zero or one; (3) if some of the initial five virgin heterozygous females died soon after being placed in the population bottle, this mortality would have no effect on the average proportions of genotypes present in the next generation except with regard to genetic drift; (4) if some of the initial males died re-

gardless of whether they were wild or mutant type, the relative proportions of wild type and mutant males in the next generation would be unaffected. The proportions of females in the various classes would be affected.

Experimental Results

Fifteen culture series, each consisting of from nine to twenty cultures, were studied. Summaries of these culture series are presented in tables 1–4. In three culture series, *y+++*, *+ctras+*, and *yctras+*, the first count was in some cases made at sixty days and in a few cases at forty-five days. All other cultures were thirty days old at first count. All counts after the first were made at thirty-day intervals. A detailed presentation of the results of study of these fifteen culture series follows.

Table 1A summarizes tests which compare the survival ability of yellow flies with wild type. This table shows that wild type flies increase in proportion while yellow flies decrease in proportion. No yellow females were observed after the third count. One culture of the twelve living at the end of this experiment contained two yellow males. The data indicate clearly that the frequency of the yellow gene is rapidly decreasing due to selective forces acting against yellow flies.

The investigations of Merrell (1949) using the same stock as was used in this experiment show that when a wild type and a yellow male compete for a given heterozygous female, the wild type male is successful in mating in 95% of the cases. These experimental data can be used to predict the proportions of the various phenotypes which are expected on the basis that 95% of all successful matings are accomplished by the wild type males in the culture. The proportions of recessive females predicted on this basis for the first, second, and third generations are .025, .014, and .008. Table 1A shows the proportions obtained at the first, second, and third counts to be .022, .029, and .008. The implication involved is that the length of time between generations and counts is the same.

The proportions of recessive females are an excellent indication of successful mating of a certain type, but the proportions of males of recessive genotype do not depend solely on definite matings for their appearance, since they can be produced by heterozygous females regardless of the male parent. The proportions of males obtained differed widely from the proportions predicted on the basis that 95% of all successful matings are made by wild type males.

Results of +ct++ culture series

Table 1B summarizes results which compare the survival ability of cut winged flies competing with wild type. Here, the proportions of wild type flies increase even more rapidly than in the case of yellow.

Merrell (1949) found that when a wild type and a cut male compete for a heterozygous female, the wild type male is successful 87% of the time. Cut males are reported to be more successful at mating than yellow males, yet selection against cut is more severe than selection against yellow. This indicates that factors other than mating success are involved, but at present they are unspecified.

Results of ++ras+ culture series

Table 1C summarizes experiments which test the ability of *ras* flies to compete with wild type for survival. Here it is clear that the situation differs from both yellow and cut since the proportions of males of both wild type and *ras* remain at approximately equal numbers in all counts after the first. Wild type females comprise about 75% while *ras* females make up about 25% of the female population.

Equilibrium is attained in a population when a state of balance is reached between opposing forces. These forces, in the case of genes, are the influences which tend toward gene loss or fixation.

TABLE 1. *Single mutant stocks competing with wild type*

A. Yellow body color versus wild type

Count	Number of cultures	Males			Females		
		Number of flies	Proportions		Number	Proportions	
			++++	*y*+++		++++	*y*+++
1	16	544	.667	.333	685	.978	.022
2	16	982	.773	.227	1190	.971	.029
3	16	792	.866	.134	1078	.992	.008
4	16	404	.923	.077	488	1.000	—
5	15	794	.972	.028	821	1.000	—
6	12	347	.994	.006	386	1.000	—

B. Cut wings versus wild type

			++++	+*ct*++		++++	+*ct*++
1	9	190	.679	.321	261	.992	.007
2	9	266	.868	.132	369	.997	.003
3	9	329	.912	.088	501	.998	.002
4	9	232	.987	.013	236	1.000	—
5	9	412	1.000	—	421	1.000	—
6	9	366	.997	.003	418	1.000	—

C. Raspberry eye color versus wild type

			++++	++*ras*+		++++	++*ras*+
1	13	396	.452	.548	448	.587	.413
2	13	636	.516	.484	721	.720	.280
3	13	657	.499	.501	779	.761	.239
4	13	589	.565	.435	649	.730	.270
5	12	476	.504	.496	486	.765	.235
6	13	643	.490	.510	633	.735	.265

D. Forked bristles versus wild type

			++++	+++*f*		++++	+++*f*
1	16	629	.529	.471	875	.862	.138
2	16	637	.669	.331	883	.810	.190
3	16	1146	.675	.325	1188	.891	.109
4	15	692	.721	.279	806	.893	.107
5	14	199	.734	.266	252	.865	.135
6	15	738	.696	.303	691	.873	.127

Summarized results of competition between flies having a single mutant gene and wild type in a series of population bottles. The initial population of each bottle was started at a gene frequency of 0.5. Counts were made at thirty-day intervals.

A culture series is considered to be in equilibrium even though individual cultures depart widely from the equilibrium gene frequency of the series.

A chi square test shows close agreement existing between the expected and the observed population if the hypothesis sets up equilibrium conditions at a gene frequency of 0.5 for this culture series. Since a state of balance is permanent, within the limits of the experiment, equilibrium is maintained between the proportions of ++*ras*+ and wild type flies in this culture series. This explanation of equilibrium, in which the components may be far from the general gene frequency, is

TABLE 2. *Double mutant stocks competing with wild type*

A. yct++ *versus wild type*

Count	Number of cultures	Males: Number of flies	Males: Proportions of phenotypes ++++	y+++	+ct++	yct++	Females: Number	Females: Proportions of phenotypes ++++	y+++	+ct++	yct++
1	11	273	.641	.088	.063	.209	528	1.000	—	—	—
2	11	504	.911	.050	.008	.032	676	.999	—	—	.001
3	11	803	.902	.071	.009	.017	911	.997	.001	.001	—
4	11	783	.959	.033	.004	.004	854	1.000	—	—	—
5	11	609	.976	.016	.008	—	584	1.000	—	—	—
6	11	784	.997	.003	—	—	636	1.000	—	—	—

B. y+ras+ *versus wild type*

			++++	y+++	++*ras*+	y+*ras*+		++++	y+++	++*ras*+	y+*ras*+
1	10	207	.449	.106	.150	.295	333	.961	.006	.018	.015
2	10	795	.670	.077	.102	.151	891	.893	.007	.097	.003
3	10	653	.625	.066	.210	.100	736	.925	—	.071	.004
4	10	767	.705	.029	.218	.048	742	.907	—	.093	—

C. y++f *versus wild type*

			++++	y+++	+++*f*	y++*f*		++++	y+++	+++*f*	y++*f*
1	7	165	.388	.224	.182	.206	229	.934	.017	.017	.031
2	7	215	.591	.158	.172	.079	219	.840	.023	.123	.014
3	7	435	.513	.133	.262	.092	302	.888	.012	.094	.006
4	7	326	.653	.101	.206	.040	335	.928	—	.072	—

D. +ctras+ *versus wild type*

			++++	+*ct*++	++*ras*+	+*ctras*+		++++	+*ct*++	++*ras*+	+*ctras*+
1	13	205	.610	.005	.098	.273	391	.905	—	.038	.056
2	13	561	.763	.005	.082	.144	758	.907	.003	.058	.033
3	13	539	.746	.009	.119	.119	617	.976	.002	.018	.005
4	13	266	.838	.008	.116	.038	304	.960	—	.039	—
5	12	384	.880	—	.117	.003	382	.960	—	.039	—
6	12	209	.923	—	.067	.010	275	.978	—	.022	—

E. +ct+f *versus wild type*

			++++	+*ct*++	+++*f*	+*ct*+*f*		++++	+*ct*++	+++*f*	+*ct*+*f*
1	9	91	.516	.099	.275	.110	188	.995	—	.005	—
2	9	372	.801	.019	.148	.032	541	.906	.013	.081	—
3	9	191	.780	.021	.173	.026	320	.941	—	.059	—
4	9	187	.813	.005	.182	—	319	.962	—	.038	—

F. ++rasf *versus wild type*

			++++	++*ras*+	+++*f*	++*rasf*		++++	++*ras*+	+++*f*	++*rasf*
1	15	617	.549	.078	.063	.310	871	.821	.053	.014	.113
2	15	741	.629	.090	.055	.225	1080	.861	.073	.020	.045
3	15	692	.675	.108	.095	.121	667	.868	.055	.045	.031
4	15	815	.729	.119	.080	.072	989	.926	.049	.019	.006
5	14	222	.712	.180	.068	.041	253	.905	.063	.012	.020
6	14	948	.726	.167	.061	.046	914	.888	.100	.010	.002

Summarized results of competition between stocks having two mutant genes and wild-type flies in a series of population bottles. The initial population of each bottle was started with each gene at a frequency of 0.5. The X chromosome bearing the two linked marker genes therefore also had an initial frequency of 0.5. Counts were made at thirty-day intervals.

TABLE 3. *Triple mutant stocks competing with wild type*

A. yctras+ *versus wild type*

Count	Number of cultures	Number of flies	Males: Proportions of phenotypes ++++	y+++	+ct++	++ras+	yct++	y+ras+	+ctras+	yctras+
1	13	461	.796	.050	—	.080	.006	.002	.017	.048
2	13	628	.798	.048	.005	.075	.003	.008	.018	.046
3	13	803	.811	.031	.004	.113	.005	.001	.017	.016
4	13	853	.877	.035	—	.062	.001	.006	.009	.009
5	13	378	.871	.016	—	.098	—	.008	—	.008
6	13	735	.914	.012		.069	.001	.001	.001	—
			Females							
1	13	788	.995	—	—	.005	—	—	—	—
2	13	1079	.983	.001	—	.013	—	—	.001	.002
3	13	954	.965	—	—	.034	—	—	—	.001
4	13	944	.987	—	—	.010	—	—	—	.003
5	13	413	.983	—	—	.017	—	—	—	—
6	13	752	.984	—	—	.016	—	—	—	—

B. y+rasf *versus wild type*

			Males: ++++	y+++	++ras+	+++f	y+ras+	y++f	++rasf	y+rasf
1	8	332	.295	.123	.027	.072	.060	.015	.175	.232
2	8	247	.563	.101	.069	.053	.056	—	.081	.077
3	8	453	.574	.073	.071	.093	.018	.011	.130	.031
4	8	256	.641	.043	.059	.066	.012	.012	.164	.004
			Females							
1	8	382	1.000	—	—	—	—	—	—	—
2	8	324	.836	.012	.062	.040	—	—	.049	—
3	8	573	.927	—	.019	.028	—	—	.026	—
4	8	232	.871	—	.047	.026	—	—	.056	—

a simple and logical extension of the concept of equilibrium existing in a single undivided population. The significant departure from equilibrium conditions in individual cultures is attributed to fluctuations in gene frequency due to genetic drift.

The results of Merrell (1949) indicate that raspberry males are half as successful as wild type males in fertilizing females of either genotype. Other factors must be involved under the conditions of this culture series, since raspberry flies are maintained in equilibrium at a gene frequency of 0.50.

Results of +++f culture series

Table 1D shows results derived from experiments to test the survival ability of forked in comparison with wild type. In counts after the second, namely, the third to the sixth inclusive, approximately 90% of the females were wild type, while the remainder had forked bristles.

A chi square test on the basis that equilibrium for this culture series was established at $p = 0.67$ and $q = 0.33$, shows that departures from the theoretical values are real during the first and second counts. This result is attributed to the fact that equilibrium for the culture

series is not immediately attained since the initial population was started with a gene frequency of 0.5. All counts after the second do not differ significantly from the equilibrium conditions postulated for this culture series.

The proportion of wild type and $+++f$ males in each culture of this series was tested to determine whether each culture conformed to the equilibrium conditions of the culture series. (One culture of the sixteen in this series reached fixation for wild type before or about the time of the first count. This culture was excluded.) In every count, except the fifth, the individual cultures showed highly significant deviations from the culture series equilibrium. The results of the fifth count indicate that in 96% of samples of this size the deviations found by chance would be as large or larger than those observed. In other words, the hypothesis that the males were present in the proportion 0.67 wild type and 0.33 $+++f$ was supported

TABLE 3.—*Continued*

C. yct+f *versus wild type*

Count	Number of cultures	Number of flies	Males: Proportions of phenotypes ++++	y+++	+ct++	+++f	yct++	y++f	+ct+f	yct+f
1	9	175	.400	.046	.017	.143	.109	.023	.040	.223
2	9	123	.756	.073	.008	.154	.008	—	—	—
3	9	546	.727	.059	.005	.189	.002	.015	.002	.002
4	9	206	.791	.097	—	.107	—	.005	—	—
Females										
1	9	390	1.000	—	—	—	—	—	—	—
2	9	180	.944	—	—	.055	—	—	—	—
3	9	733	.980	—	—	.019	—	—	.001	—
4	9	196	.949	.005	—	.046	—	—	—	—

D. +ctrasf *versus wild type*

			Males: ++++	+ct++	++ras+	+++f	+ctras+	++rasf	+ct+f	+ctrasf
1	14	484	.463	.016	.004	.116	.078	.052	.004	.267
2	14	547	.766	.009	.020	.066	.037	.035	.005	.062
3	14	943	.700	.011	.020	.179	.029	.040	.001	.020
4	14	747	.736	.008	.025	.151	.023	.035	.005	.016
5	13	353	.702	—	.068	.119	.008	.093	.006	.003
6	13	390	.808	—	.067	.102	.003	.020	—	—
Females										
1	14	671	.851	.009	.001	.028	.022	.003	—	.085
2	14	866	.917	—	.025	.024	.003	.027	—	.003
3	14	1092	.949	.003	.006	.031	.001	.008	—	.002
4	14	829	.918	.001	.018	.048	.001	.013	—	—
5	13	364	.937	—	.022	.036	—	.005	—	—
6	13	423	.981	—	.002	.017	—	—	—	—

Summarized results of competition between stocks carrying three mutant genes and wild type flies in a series of population bottles. The initial population of each bottle was started with each gene at a frequency of 0.5. The X chromosome bearing the three linked marker genes therefore also had an initial frequency of 0.5. Counts were made at thirty-day intervals.

only in this count. The conclusion here, as in the case of $++ras+$ is that the significant fluctuations in gene frequency in individual cultures can be attributed to genetic drift.

The results of Merrell (1949) indicate that forked males are equally successful with wild type males in fertilizing females of either genotype. It is evident that selective forces other than mating cause a decrease in level of equilibrium from 0.50 to 0.33 for the forked gene.

Results of all other culture series

Table 5 is a summary based on inspection of Tables 2, 3 and 4. These three tables have many elements in common since competing genes start in the initial population of a culture linked together in the coupling phase. The chromosome frequency of the wild type and the recessive bearing X chromosomes is each 0.5; as a consequence it follows that the frequency of each gene carried by the recessive bearing X chromosome is also 0.5. Any linked group (of 2, 3, or 4) of the genes studied had little chance of surviving in that combination since crossing-over percentages of 20.0, 12.8, and 23.9 tended to separate these genes and increase the number and proportion of the single and smaller gene combinations at the expense of the larger linkage groups. At the left of Table 5 are listed the designated culture series. Across the top are the sixteen possible phenotypes. Phenotypes which compete with each other within the same culture are shown on the same horizontal line while those phenotypes competing with different phenotypes in different culture series are arranged in the same vertical column. Cases in which a gene was decreasing in frequency but which were interpreted as tending toward a low equilibrium level were marked $-/E$. When the gene frequency seemed to be increasing toward an equilibrium level the symbol $+/E$ was used.

The striking feature of Table 5 is the constancy of the end result of the competitive process. Raspberry and forked consistently tended towards equilibrium regardless of the other genes to which

TABLE 4. yctrasf *versus wild type*

Count	Number of cultures	Males																
			Proportions of phenotypes															
		Number	++++	y+++	+a++	++ras+	+++f	yct++	y+ras+	y++f	+dras+	+a+f	+++rasf	yctras	+dtrasf	y+rasf	yct+f	yctrasf
1	20	538	.597	.061	.002	.015	.132	.017	.004	.004	.006	—	.061	.033	.009	.002	.002	.056
2	20	795	.682	.042	.002	.062	.077	.006	.002	.002	.011	—	.038	.018	.006	.001	.002	.048
3	20	903	.754	.029	.001	.032	.107	.003	—	.012	.009	—	.027	.010	.007	—	.001	.008
4	20	1036	.827	.017	.001	.025	.072	.003	.006	.004	.004	—	.023	.008	.004	—	—	.006
5	20	656	.840	.021	—	.040	.075	—	.002	.003	.002	—	.024	.002	—	.002	—	—
6	20	1038	.831	.007	—	.046	.089	—	.002	—	.001	—	.024	—	—	—	—	—
		Females																
1	20	1110	.986	.002	—	.003	.004	—	—	—	—	—	.002	.003	.001	—	—	—
2	20	1391	.922	.006	—	.016	.050	—	—	.001	—	—	.004	—	—	—	—	—
3	20	1252	.958	.002	—	.007	.022	—	—	.003	—	—	.006	—	.002	—	—	—
4	20	1201	.972	.002	.001	.007	.013	—	.001	—	—	—	.003	—	—	—	—	—
5	20	722	.974	—	—	.004	.018	—	—	—	—	—	.004	—	—	—	—	—
6	20	1107	.966	—	—	.020	.010	—	—	—	—	—	.004	—	—	—	—	—

Summarized results of competition between *yctrasf* and wild type flies in a series of population bottles. The initial population of each bottle was started with each gene at a frequency of 0.5. The X chromosome bearing the four linked marker genes therefore also had an initial frequency of 0.5. Counts were made at thirty-day intervals.

TABLE 5. *Summary of culture series (see text)*

Table no.	Culture series	Competing phenotypes															
		++++	*y*	*ct*	*ras*	*f*	*yct*	*yras*	*yf*	*ctras*	*ctf*	*rasf*	*yctras*	*yrasf*	*yctf*	*ctrasf*	*yctrasf*
2A	*yct*	+++	−−	−−−			−−−										
2B	*yras*	+	−		E			−									
2C	*yf*	+	−			E			−								
2D	*ctras*	++		−−−	E					−							
2E	*ctf*	+		−−−		+/E					−−−						
2F	*rasf*	E			E	E						Low E					
3A	*yctras*	++	−−	−−−	E		−−	−−		−−			−−				
3B	*yrasf*	+/E	−		E	E		−−	−−			E		−−			
3C	*yctf*	+/E	E	−−−		E	−−−		−−−		−−−				−−−		
3D	*ctrasf*	++		−−	E	E				−	−−−	−/E				−−	
4	*yctrasf*	+/E	−	−−−	E	E	−−−	−−	−−	−−	−−−	Low E	−−	−−−	−−−	−−	−−−

E means at equilibrium.
+/E means increasing towards equilibrium.
−/E means decreasing toward equilibrium.
The number of +'s or −'s indicates the rate of change in frequency.

TABLE 6. *Detailed data on* y+++ *males of the* yct+f *culture series*

Count	Proportion $y+++$ present*	No. cultures in series	No. cultures having $y+++$ flies	Total no. $y+++$ males present	Number of cultures each having over 25% of total $y+++$ flies present	Total % $y+++$ flies in cultures each having over 25% of $y+++$ flies
1	.046	9	4	8	3	87%
2	.073	9	4	9	2	77
3	.059	9	6	32	2	84
4	.097	9	4	20	1	70

* Column taken from table 3C.

they were initially linked. Yellow and cut were consistently pushed toward extinction regardless of the genes to which they were initially linked. Yellow in the *yct+f* culture series seems to disagree with the other results obtained with yellow. That this difference is more apparent than real is shown by the detailed examination of the original data presented in Table 6. This table shows that the number of cultures in which the yellow flies are found decreases with increasing time. Had this culture series been continued for a longer time or had it contained a greater number of cultures, it is expected that the results would be consistent in every way with the remainder of the pertinent data of Table 5. The single culture which contains fifteen yellow flies, when the other three of the nine cultures average two yellow flies, is an excellent example of genetic drift in a direction opposite to strong selective forces.

The success of linked genes, with appreciable cross-over values, in resisting division into their components is a good indication of their survival ability while linked. The continued presence in successive counts of recessive females showing linked genes indicates that the recessive males, carrying those genes, are at least moderately successful in survival and mating. The recessive females also furnish one source of males of the linked mutant genotype for the next generation. Table 3B shows that, for the four counts involved, *rasf* flies maintain themselves better than either raspberry or forked alone. Part of the *rasf* gametes are produced by crossing over in females heterozygous for *y+rasf*. This is probably not an important source of *rasf* gametes after the second count.

In summarizing table 5 it can be said that generally combinations of linked genes survived as would be predicted from a knowledge of their separate survival success plus a knowledge of their linkage relations.

DISCUSSION

Culture conditions were closely controlled with respect to temperature (20° C.), kind and amount of culture medium, size and shape of bottle. Uncontrolled factors which differ from culture to culture can conceivably so confound experimental results as to make them valueless. In the present experiment every culture series in which *ras* was present showed that an equilibrium was soon established (table 5). Conversely, every culture series containing cut showed that this gene was rapidly eliminated. The consistent survival performance of individuals possessing these genes shows that the intrinsic qualities of the flies were far more important than existing differences between culture series conditions.

Genetic drift, i.e., random variation of gene frequency in small populations merely as a consequence of chance, has received an increasing amount of attention, since this process can account for the fixation of characters which, apparently, have no survival value. The process of genetic drift operates largely upon

genes having low (positive or negative) selection values. In discussing this concept, Wright (1943) says, "The simplest model is that in which the total population is assumed to be divided into subgroups, each breeding at random within itself. . . . Whatever the size of the subpopulations considered the variability (in gene frequency) depends upon the size of the inbreeding unit. There is an important amount of differentiation among large regions if the unit group is as small as 10, appreciable differentiation if the unit group is as large as 100, but little if it is as large as 1000. It should be said that there are important qualifications if there are other factors; mutation, rare long range dispersal or selection."

Effective population size, basic to any consideration of genetic drift, in a culture of this experiment involves: (1) the number and successful reproductive ability of adults present at counting time and, (2) the number of flies which emerge and die between counts but leave successful offspring. The hazards of reproductive success, due to non-genetic as well as genetic factors, are such that the effective breeding population is invariably smaller than the actual population. In these experiments, it is estimated that the actual population lies between two and three hundred flies (table 7). This estimate places the unit group size in Wright's middle group where appreciable genetic drift might be expected.

TABLE 7. *Number of adults present in cultures of different ages based on one count of each culture*

Culture age days	Number of cultures	Males Mean ±S.D.*	Females Mean ±S.D.*
11	8	131±51	151± 75
12	4	138±89	108± 68
17	8	102±34	130±150
22	5	112±62	109± 70
24	8	80±35	92± 63
26	5	74±30	90± 53
28	4	67±47	66± 43

* S.D. $= \sqrt{\frac{\Sigma(X)^2}{N-1}}$

The effects of natural selection are recognized by orderly population changes in gene frequency. Such changes may lead to gene loss, fixation, or equilibrium. Whatever the end, it results from consistent orderly change toward the final state. A necessary condition is that the size of the effective breeding population be large enough to preclude random gene loss or fixation. Genetic drift, a different process, is recognized by random variation in gene frequency of unit groups which depart widely from the gene frequency of the complete population. Both natural selection and genetic drift affect the populations described and though the latter proved a valuable concept, natural selection was more effective in determining gene loss or fixation.

The significance of the experiment in terms of evolution, lies in the fact that the experimental data can be explained by existing evolutionary concepts which are themselves derived by extension of the gene theory. These data show that no reasonably complete discussion of evolution is possible unless it includes consideration of effective population size since this factor alone can explain the retention or fixation of a character which may seem not only useless, but even harmful to survival.

CONCLUSIONS

1. Natural selection rapidly eliminated the gene for yellow body color from a population under the conditions of this experiment.

2. The gene for cut wings was eliminated from a population even more rapidly than the gene for yellow body color.

3. No evidence against the view that the gene determining raspberry eye color was maintained in equilibrium at a gene frequency of 0.50 was found, although individual cultures of the raspberry culture series showed significant deviations from the equilibrium gene frequency. This is believed to be due to genetic drift.

4. No evidence against the view that the gene determining forked bristles reached equilibrium at a gene frequency

of .33 in the forked culture series was found, although here, as well as in *ras*, individual cultures showed significant deviations from the culture series equilibrium.

5. In general, the interactions of the various combinations of these four genes in terms of survival values were what would be predicted from a knowledge of the survival properties of each of the genes separately, plus knowledge of their linkage relations.

6. Genetic drift proved a useful concept in explaining certain observed changes in gene frequency, but selection was a far more effective force in determining the loss or fixation of a given gene in these populations.

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DISTRIBUTION PATTERNS OF THE GENERA OF LEAFY HEPATICAE OF SOUTH AMERICA [1, 2]

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INTRODUCTION

These studies were undertaken to determine the distribution patterns of the *genera* of living Hepaticae, and to ascertain whether these patterns might also reflect something of the past developmental history of the group and of the vegetation of the earth. Already studies by Müller (1912–16), Domin (1923), Evans (1934), Herzog (1926) and others have indicated that the areas of distribution of individual *species* of Hepaticae are as sharply delimited and present as varied patterns of distribution as do many of the Phanerogams. The species of Hepaticae do not, therefore, show a uniformly cosmopolitan distribution, a characteristic which has been erroneously assigned to them and to other groups of spore-bearing plants.

The Hepaticae comprise a group of perhaps 8,500 species,[3] both leafy and thallose forms. Of these, the leafy forms constitute 7,200 species or about 85%. They have been classified into 18 families (see Evans, 1939, for the detailed list), but it may be that this is too conservative an interpretation, particularly among those groups which represent the more primitive types. There are at present approximately 180 genera of leafy forms. The relatively small number of Hepaticae (leafy and thallose forms), and the fact that they as a group are very old, would seem to make them promising materials for research relating to problems of plant distribution.

A distribution map was made for each genus from all the published records. In this type of study the species concept held by an author would have little effect on the distribution pattern of a genus; whether one recognizes 15 species or only 5 species, the over-all distribution based on those specimens is the same. At the present time this is the only type of approach practical in the study of the distribution of most of the larger genera outside of North Temperate areas, particularly of the tropics, since most of the genera outside of the North Temperate Zone are in need of systematic study and necessarily of revision. For this reason it is not justifiable to make a study of

[1] A part of the data in this paper was presented to the Section on Cryptogams, 7th International Botanical Congress, Stockholm, Sweden, in July, 1950.

[2] I wish to acknowledge research funds from the Ohio Academy of Sciences and from the Graduate School of Arts and Sciences, University of Cincinnati, for use in this project; I also wish to acknowledge the assistance of Mr. Robert Boller in the making of more than 500 maps. To Dr. E. Lucy Braun, Dr. W. H. Camp, Dr. K. Caster, and Dr. J. H. Hoskins, who have made suggestions and criticisms, I am particularly indebted.

[3] The classification of the Hepaticae followed here is that of Evans (1939). There are four orders: 1) Jungermanniales, which includes the Haplomitrineae (leafy plants in 2 genera with 5 species—the Calobryales of some authors), the Jungermanniales Acrogynae (leafy plants in approximately 180 genera and some 7,200 species —the Jungermanniales of some authors), and the Jungermanniales Anacrogynae (thallus plants in about 22 genera containing 550 species —the Metzgeriales of some authors); 2) Marchantiales (with approximately 400 species in 32 genera, all thalloid); 3) Sphaerocarpales (with approximately 20 species in 3 genera, all thalloid); and 4) Anthocerotales (with approximately 320 species in 5 genera, all thalloid). The radial leafy forms come first and are followed by the dorsi-ventral leafy forms and then the thallose forms. For a detailed survey of liverworts and a discussion of the characteristics of these subdivisions and the relationships of the Hepaticae, the reader is referred to Castle (1946).

the distribution of the *species* in the latter groups at this time.

The Hepaticae are of special interest not only in themselves, but because they have played so conspicuous a rôle in the conjecture which has culminated in the various patterns of phylogeny in the plant kingdom. Unfortunately, the fossil record is all too incomplete to furnish more than a hint of the age, the past distribution, or the developmental history of the group in the far past, but what has already come to light is indeed significant. Then, too, there are several interpretations of the morphological facts at hand with respect to the developmental history within the group (Fulford, 1948) so that even here the picture is incomplete.

The Fossil Record of Hepaticae

The earliest known fossil hepatics are those which Walton (1925, 1928) described from the Middle and Upper Carboniferous. Four of the species belong to the Jungermanniales Anacrogynae (*Hepaticites Kidstoni, H. Langi, H. lobatus, H. metzgerioides*), and the fifth one (*H. Willsii*), has been transferred to the form genus *Thallites,* since the characters are rather indistinct. More recently Walton (1949) has described another from the Coal Measures of Clackmannanshire. This then is proof that already in the late Paleozoic the Anacrogynae had come into being, and that several thallus patterns had become established, at least in the Northern Hemisphere. Whether or not this particular group is mono- or polyphyletic in origin cannot possibly be determined from the living members, for the latter are highly diversified and specialized in one way or another; nor can any very close relationships between fossil and living members be established until fruiting material of the fossils is found. All that we can say at this time is that Hepaticae of the anacrogynous type did exist during the Coal Measures (some of them with as much thallus differentiation as is present in the more advanced of the living forms, namely in *Metzgeria* and *Treubia*).

The record since the close of the Paleozoic is more diversified for marchantiaceous and leafy forms are found in addition to members of the Anacrogynae.

The Upper Triassic and the Jurassic beds have yielded at least six thallose forms belonging to the Marchantiales or the Anacrogynae, from regions as widely separated as Japan, England, the Urals, France, Silesia, Poland and Siberia. To this group must be added the species of *Marchantites* which Halle (1913b) found in the Jurassic–Lower Cretaceous beds of Patagonia. Too, the careful studies by Harris (1931, 1937, 1942) have revealed 5 species of Anacrogynae from Greenland and 2 from England.

Furthermore, Harris (1938, 1939) has demonstrated that the long recognized *Naiadita lanceolata* Buckm. of the British Rhaetic Flora (Triassic) should be included among the leafy liverworts. The leaves were similar to those of plants of the living primitive genus *Calobryum,* the sporophyte was partly sunken in the stem in such a way that the lower half of the capsule was covered by the calyptra and part of the stem, apparently coalesced in a manner somewhat similar to that in *Gymnomitrium* (Knapp, 1930, fig. 104). This arrangement is considered an advanced or at least a specialized condition, rather than a primitive type. Thus, already at the time when *Naiadita* flourished, at least some leafy liverworts had reached a high degree of specialization.[4]

This evidence thus indicates the very important fact that by the end of Jurassic time the Hepaticae had already become diversified into the major groups as we now know them, Marchantiales, Anacro-

[4] Another fossil plant, *Schizolepidela gracilis* Halle from the Mid-Jurassic of Hope Bay, Graham Land, Antarctica, may also be a leafy liverwort. Dr. Halle (1913a) described it and stated that it was of uncertain affinity and therefore did not assign it to any known group of plants. The size, growth habit and leaf characteristics suggest an hepatic with bilobed leaves, but until further morphological evidence is forthcoming, its relationships must remain uncertain.

gynae and Acrogynae (Jungermanniales), and into at least several diverging lines in these groups. They were widespread in the Northern Hemisphere and were also probably equally widespread in the Southern Hemisphere, although at the present time fossil remains have been found in only one area.

The Cretaceous record includes 5 or more thalloid species from the present Arctic and cold and warm temperate sections of North America, and from Portugal. No leafy forms have as yet been reported.

The Tertiary record is more complete. From the Eocene there are reports of 5 thallose forms from areas in the United States and in France, and of two leafy species from the United States (Colorado and Texas).

One anacrogynous form is reported from the Oligocene of France and one from Germany. More than two dozen different leafy species have been reported from the ambers of the Baltic, most if not all of which have been referred to living genera of the Northern Hemisphere. Whether one agrees with these determinations or not, this fact remains:—at that time numerous diversified forms of leafy hepatics did exist, all of them very similar to if not identical with members of the most specialized living groups, e.g. *Frullania, Radula, Scapania, Lejeunea* and *Jungermannia* forms (Gottsche, 1886). It also indicates that the rate of change among these forms is very slow, as Müller (1939–1940) has pointed out.

From the Miocene one thalloid and one leafy species have been reported from the United States, and two thalloid and two leafy species from France. These latter show a *Plagiochila asplenioides*-like habit. There is only one record from the Pliocene, a marchantiaceous form from France.

The Quaternary forms are numerous, and all of them are referable to present-day species.

In all, from the Coal Measures through the Pliocene, there are at least 20 records of species of the marchantiaceous-anacrogynous type; 14 or more records of species belonging without doubt to the Anacrogynae; and at least 6 records in addition to those in the amber, of leafy forms. This is a total of more than 50 records. Of course, further morphological study may exclude certain of these fossils (some thallus forms) from the Hepaticae, but the many unmistakable fossils of Marchantiales, Anacrogynae, and the leafy forms, included in this record leave no doubt as to the presence of the Hepaticae in the floras from the Upper Carboniferous time to the Present.

The meager record of fossil Hepaticae in the Southern Hemisphere might of course mean that the hepatics were absent from most of the floras of the past in that area, or it might mean that they were very scarce or absent in the localities where these fossil floras have been investigated. It more probably means that they have been overlooked in the fossil beds.

Certain Considerations Pertaining to the Problem

If we take into consideration the fossil record, meager though it is, together with the morphological facts as presented in the living group, the types of evolutionary trends which are evident in this and in other groups of living plants (including the many reduction series), and the general principles on which our concepts of evolution are based, it seems to me that the only possible conclusion is that the living Hepaticae represent a polyphyletic group, and that at the present time there are many lines of descent represented in the living flora. Some of these have developed primarily or exclusively in the Northern Hemisphere, others primarily or exclusively in the Southern. The development within the different lines is not uniform and the various lines have attained different levels of complexity, in part at least, related to the geological age of the appearnce of that line. The points to be kept in mind then in the interpre-

tation of the distribution patterns of the leafy Hepaticae may be outlined as follows:

1. The Hepaticae as a group seem at an early age to have attained the general and diversified lines of development which we know today; the Anacrogynae had evolved to forms similar to some of the more advanced living genera by Upper Carboniferous time; the marchanteaceous and leafy forms were present in the Triassic.

2. The sporophyte of the earliest known leafy form, *Naiadita,* was as much specialized as are some specialized living forms. This means that in addition to being old, at least certain structures of hepatics have changed very little in the long time from the Upper Carboniferous or Triassic to the present.

3. In many groups of the living forms evolution has progressed very slowly, and at a rate very much slower than among the flowering plants. Most of the groups of hepatics react as old groups which are not aggressive, similar to Ginkgo, cycads, and Sections of the podocarps.

4. Since hepatics occupy microhabitats, these plants then are actually subjected to a climate, a microclimate, which might be considerably different from the general climate of the area.

5. Hepaticae have thus been able to persist in areas in which the larger plants and animals with which they were originally associated have long since disappeared. There are many local examples of this.

6. Because the Hepaticae do maintain themselves so well in microhabitats and because they do "change" so slowly, it is my contention that living hepatics better than other groups of living plants might serve as "indicators" of past climates, past migration routes, and paleogeography.

7. By this same reasoning, too, it might be possible to reconstruct from the present day distributional patterns of selected groups of living Hepaticae, something of the past history of their migration routes and also something of the possible locale of origin of the various groups.

Distribution Patterns of the Living Genera of Leafy Hepaticae in the Southern Hemisphere

The genera of leafy Hepaticae occurring in the Southern Hemisphere today, particularly in South America, may be grouped according to their distribution patterns in the following manner:

A. Cosmopolitan and Subcosmopolitan Genera
B. Endemic Genera
C. Genera with a marked Discontinuous Distribution
   1. Bipolar Disjuncts
   2. Disjuncts between South America and other lands of the Southern Hemisphere
      a) Tropical Genera
      b) Subtropical / tropical—Temperate—Antarctic Genera
      c) Antarctic Genera

A. The Cosmopolitan Genera, widespread throughout the world in all the floristic zones, and the Subcosmopolitan Genera, widespread throughout the Southern Hemisphere and to some extent in the North, need no special comment. Their wide distribution indicates that individually they are capable of wide adaptability, the nature of which can be determined only through detailed experimentation. *Plagiochila* with more than 1,200 so-called species is one of the most conspicuous of these. Figure 1 shows the distribution of this genus. It also shows something of the "distribution pattern" of collectors. Actually, hepatics have been collected in practically all of the areas where flowering plants and ferns have been collected, a point of no small significance in the consideration of a more restricted distribution. Among the other genera which might be included in this group are *Frullania,* with about 500 species, *Herberta,* with about 100 species, *Lophocolea,* with about 350 species, *Chilo-*

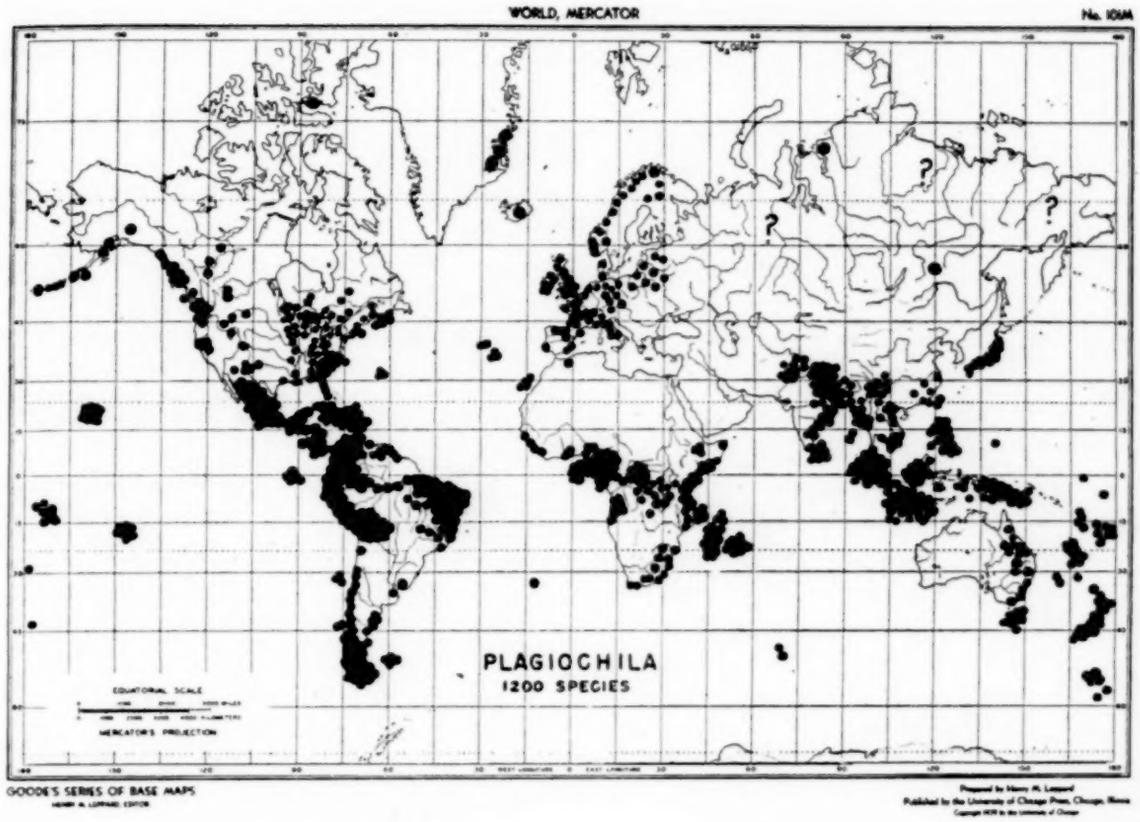

FIG. 1. Map showing the distribution of *Plagiochila*, a cosmopolitan genus of some 1,200 species.

scyphus, with about 165 species, and *Radula*, with about 250 species.

B. Endemic Genera. By an endemic is meant "any species or other taxonomic unit which is so distributed as to be confined to one particular country or region" (Good, 1947, p. 48). It would seem that this group might be made up of three sorts of genera: the first, aggressive genera of wide adaptability, probably young geologically, which have not as yet become widespread; the second, stable, unaggressive genera which once were more widespread, doubtless old geologically, the so-called "climatic relics" (Wulff, 1943, p. 79); and third, recent or old genera so *highly specialized* that they just manage to maintain themselves in a limited habitat.

The first group includes genera which appear to be highly adaptive, often with a rather large number of species, which are widespread in one area but in which a more far-reaching spreading out has not taken place because of the short time since the genus had evolved or because of geographical barriers. Available records show that the following Tropical and South American genera probably belong to this group: *Micropterygium*, 16 species of tropical South America; *Stephaniella*, 3 species of South and Central America; *Apotomanthus*, 1–2 species of Central and tropical America and the West Indies; *Anoplolejeunea*, 3 species of the West Indies, Central and tropical South America; *Cyclolejeunea*, about 20 species of the West Indies, Central and tropical South America; *Cyrtolejeunea*, 1–2 species of the West Indies and northern South America; *Macrolejeunea*, 5 species of the West Indies and tropical South America; *Neurolejeunea*, 3 species of the West Indies, Central America and northern South America; *Omphalanthus*, 3 species widespread in the West Indies, Central and tropical South America; and *Potamolejeunea*, 8 species of Central and northern South America.

The second group of endemic genera

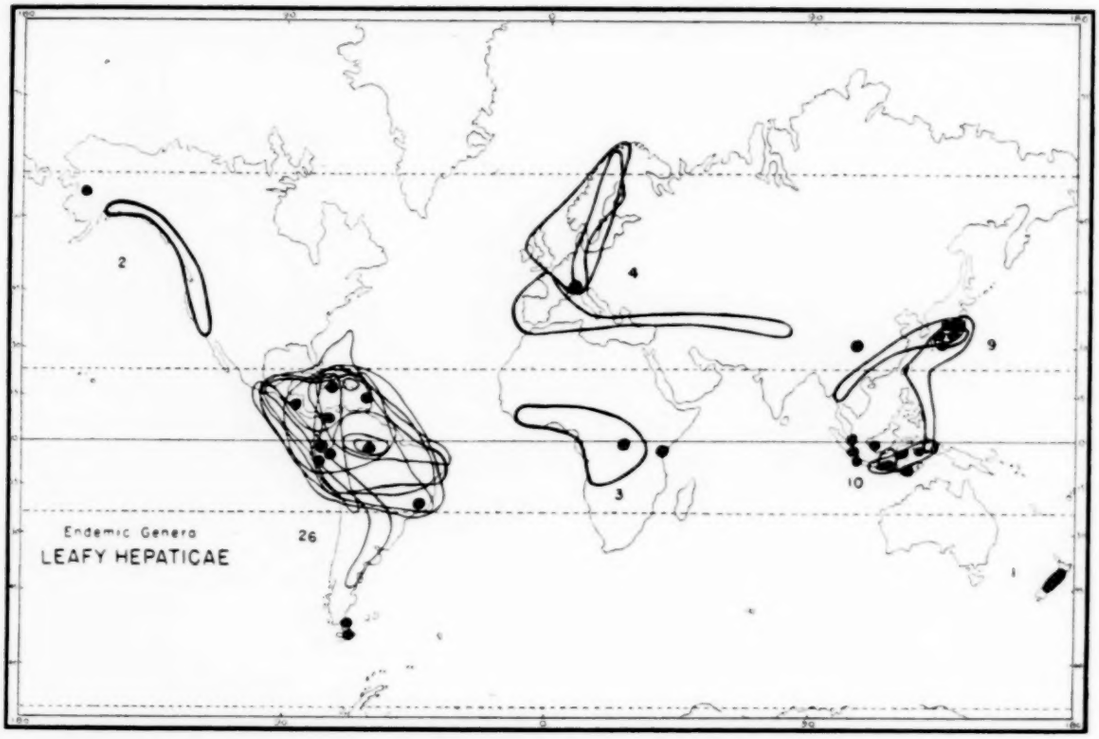

FIG. 2. Map showing the distribution of the endemic genera throughout the world.

includes those which are probably old in point of geological time of origin, and which are scarcely able to be aggressive in becoming adapted to the more recently evolved climates and habitats. They have thus died out over much of their former ranges except in local areas where the microhabitats and their microclimates have remained unchanged and stable or nearly so; they may also have once occupied areas since completely destroyed but may have migrated out before the complete extinction of the species in those areas. Some may have come from Antarctica. They might well be designated "climatic relics." Of course, some of these genera could be of relatively recent origin but, because of limited time or a certain high degree of specialization could have been unable to spread widely. The latter come within the third group. Because of the absence of a fossil record for any of these, it is impossible to demonstrate whether any of the endemic genera were actually more widespread or are of great age. It would seem that a combination of primitive characters together with some highly elaborated or specialized ones might in a general way be considered as indicative of a "unit" of great age, and under the present circumstances, on the way to extinction. I have included 14 genera of Tropical and South America in the second and third groups. They are, for the most part, monotypic, and include: *Anomoclada,* from the Amazon; *Blepharidophyllum,* from Patagonia; *Chaetocolea,* from Ecuador; *Mnioloma,* from Costa Rica; *Mytilopsis,* from Peru; *Pigafettoa,* from Patagonia; *Protocephalozia,* from the Amazon; *Pteropsiella,* from the Amazon; *Amblyolejeunea,* from Guadeloupe; *Cystolejeunea,* from the West Indies; *Leiolejeunea,* from Jamaica; *Myriocolea,* from Ecuador; *Myriocoleopsis,* from Brazil; and *Sphaerolejeunea,* from Colombia.

The endemic genera of the world, 55 in number,[5] are, according to present

[5] Recent papers by Th. Herzog, Trans. British Bryol. Soc. 1(4): 275–326. 38 fig., 1950, and Soc. pro Fauna et Flora Fennica, Mem. 25: 43–72. 20 fig., (1948–49) 1950, added two endemic genera, one in South America and one in Borneo.

knowledge (see fig. 2), distributed as follows: 2 genera in western North America; 4 in Europe and the Mediterranean; 9 Sino-Japanese (4 of these are *Lejeuneaceae* and belong with the tropical Southern Hemisphere group); 10 are in the Malayan Archipelago (mostly local); 1 is limited to New Zealand; 3 are in tropical Africa; and 26 are limited to tropical and South America. Of these last 26 genera, 4 are Caribbean, 4 Brazilian, 4 Andine, 12 are widespread and 2 are Patagonian.

It would seem of particular significance that nearly half of the endemic genera are confined to South America and adjacent Central America and Caribbean areas. Many of these, because of their high degree of specialization and because of certain primitive characters, suggest a great age. The next highest number is the 10 genera of the Malayan Archipelago region. These genera are monotypic but, for the most part, their characteristics are such that a more recent origin is indicated. It is surprising that the New Zealand area has yielded only one endemic genus, *Goebeliella*.

A further examination of these endemics shows that, of the 55 genera, only 11 at most are truly northern, and the remaining 44, or 80%, occupy in a general way the former southern land mass or masses. To reiterate, 26 of these 44 genera belong to Tropical and South America (14 are members of the *Lejeuneaceae*). Camp (1947, p. 179 and fig. 31) and Good (1947, p. 131) have pointed out that among the flowering plants there are twice as many endemics in the Southern Hemisphere as in the Northern Hemisphere. The Hepaticae show this same trend to an even greater degree.

If endemism is in any way indicative of centers of origin, as has been suggested by many, these figures are indeed significant. On the other hand, since the Hepaticae represent a very old group which was present in forms similar to our present-day *Orders* (perhaps even genera), in Mesozoic times, the low number of endemics in the Northern Hemisphere is important only within limits—since Pleistocene glaciation in part of the Northern Hemisphere precludes the survival of endemics in a part of the area. But, on the other hand, the flora of Antarctica has recently been destroyed also.

If one compares the numbers of endemic hepatics in the various continents of the Southern Hemisphere, South America again leads the list both in limited or local and in widespread endemics!

C. Genera with a Marked Discontinuous Distribution. By discontinuous distribution is meant the occurrence of a genus in two or more separate areas—often widely separated. Obviously, any genus which is widespread in the Southern Hemisphere shows a discontinuous distribution by the very nature of the distribution of the land masses, but the term is used here for those genera in which the distribution is more or less limited on each of the land masses under consideration. The question at once arises as to whether this pattern is to be looked upon as the result of a polyphyletic origin of the genus in question, or a monophyletic origin of a genus which once had a widespread continuous area of occupancy including either the present disjunct localities, or, at least, the possible migration routes to the present areas occupied. The latter view seems the more acceptable in the light of our present knowledge of genetics and the origin of taxa.

The genera of leafy Hepaticae of the Southern Hemisphere showing a discontinuous distribution which includes South America may be divided into 1) Bipolar disjuncts, and 2) Disjuncts between the widespread lands of the Southern Hemisphere.

1) Bipolar Disjuncts. These include "taxonomic units distributed both in the boreal and in the austral zone but absent from the tropical lowlands, with or without intermediate populations in tropical mountain areas" (Du Rietz, 1940, p.

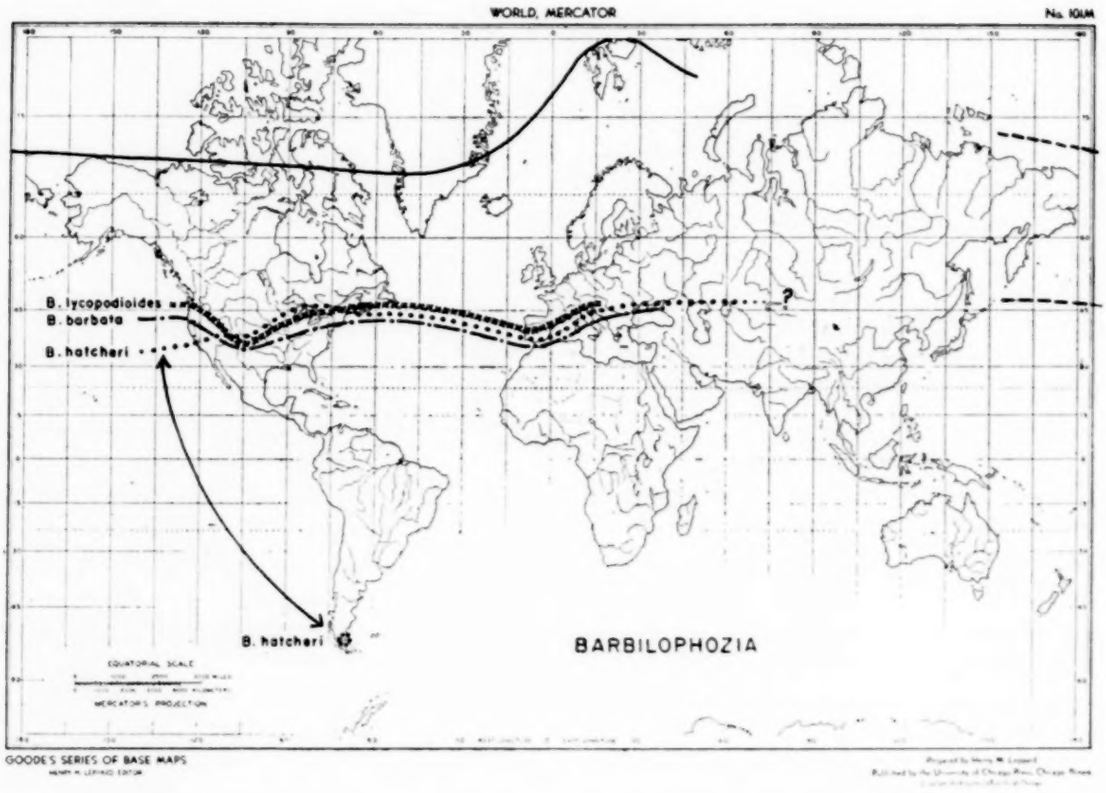

FIG. 3. Map showing the distribution of *Barbilophozia*, a genus of 3 species which shows a bipolar distribution. It is predominantly of the Northern Hemisphere but one of the species also occurs in Patagonia.

226). Du Rietz, Irmscher (1922, 1929), Cain (1944) and others have written at length concerning the possible interpretations of this pattern and the ways and means by which it may have come about. A number of hepatics may be added to the already long list of plants which show this distribution. It must be kept in mind that this distribution pattern among these genera has probably not always come about in the same way, from the same causes, or during the same geological epoch or even period, and certainly no single explanation will serve for even the few described here. Too, some of these genera must have originated in the Northern Hemisphere and some in the Southern. The four genera described here will serve to illustrate this type of distribution.

Barbilophozia (fig. 3) is a small genus of three species which is circumpolar in the Northern Hemisphere and doubtless has originated from a phyletic line of the Northern Hemisphere. One of the species, *B. Hatcheri* (Evans) Loeske, also occurs in southern Patagonia. The genus appears to be of rather recent origin.

Lepicolea (fig. 4), a genus of about 14 species, includes one group which occurs in New Zealand, the Malayan Archipelago, and Japan; another in South America along the Andes from Patagonia to Colombia and Central America, with one of the southern species also in Africa; and one northern species recently described from St. Lawrence Island, Bering Sea. The genus is of southern origin and belongs to a primitive family.

Blepharostoma (fig. 5) is a genus of about 13 species. One species is widespread throughout the temperate and arctic Northern Hemisphere, one is a local endemic along the west coast of North America, one is endemic in Sikkim, and the others occur in southern South America or in New Zealand-southeastern Australia with one species common to both areas. This represents a third type of

distribution pattern, where a genus of southern origin has become very widespread in the Northern Hemisphere, in part since glaciation. This genus, too, belongs to a primitive family.

The genus *Anastrepta,* with a species in the Northern Hemisphere in the Himalayas, China, Japan, Hawaii, Alaska and throughout Europe, one in Sikkim, and two in Patagonia, is still another example of this bipolar pattern.

2) Disjuncts between South America and the other lands of the Southern Hemisphere—including the Nepal-Sikkim area of India. According to the fossil evidence at hand, India was once in free continental communication with all the present large land areas of the Southern Hemisphere. It is well understood that the floras of these continents have not been explored as fully as they might be, that with few exceptions the genera are in need of monographic revision, and that there are large and important collections which have not yet been studied. On the other hand, as was indicated by the distribution of the genus *Plagiochila* (fig. 1), much of the area has been sampled—at least casually, and the number of collections has been large.

It is of interest to note also that, although in a large part the general patterns are identical with those of certain of the vascular plants, the Hepaticae seem to supply in addition more of the needed detail and some of the intermediate steps never or no longer present among the more recent, expanding, and more aggressive flowering plant group. It must be kept in mind that at the time when, according to the fossil evidence, major phyletic lines of the Hepaticae had already become differentiated (Upper Carboniferous and Triassic), the flowering plant lines *per se* were not yet recognized in the world flora, so that while the former had already reached a level of high evolutionary development in their group, the latter as a group must have been represented only by their primitive precursors. And while the past history which we are attempting to reconstruct through

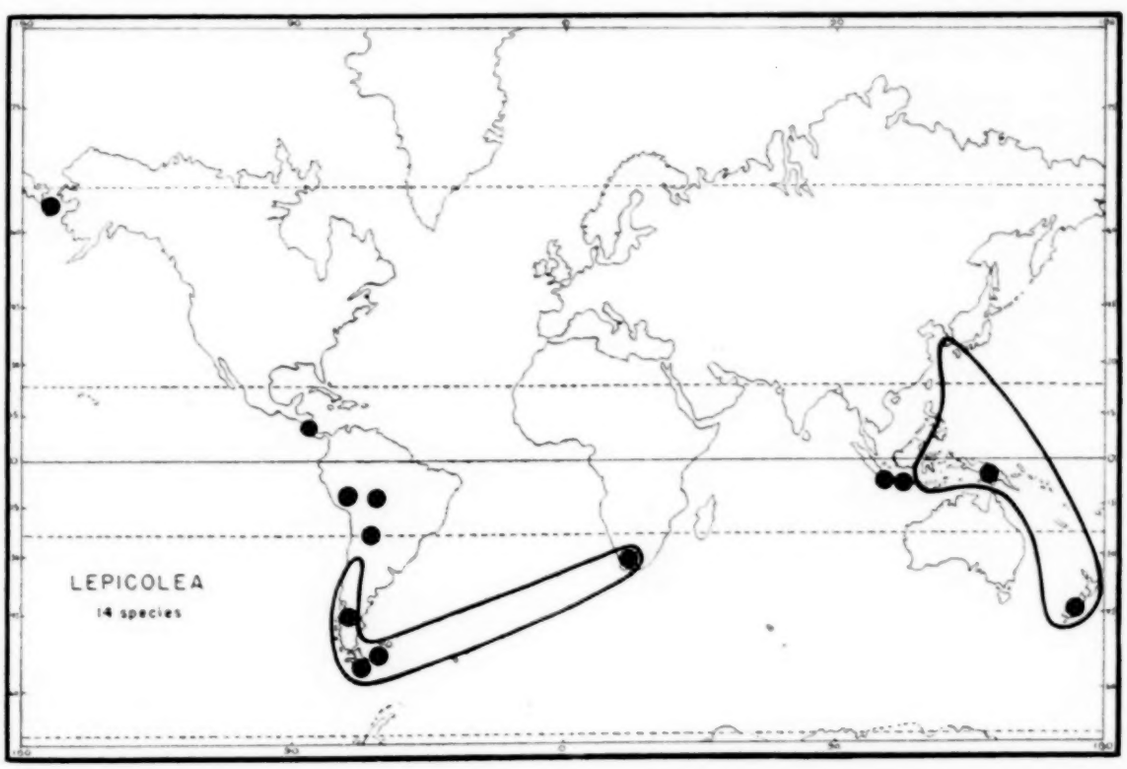

FIG. 4. Map showing the distribution of *Lepicolea,* a genus showing a bipolar distribution. It is predominantly of the Southern Hemisphere but one disjunct species occurs on St. Lawrence Island, Bering Straits.

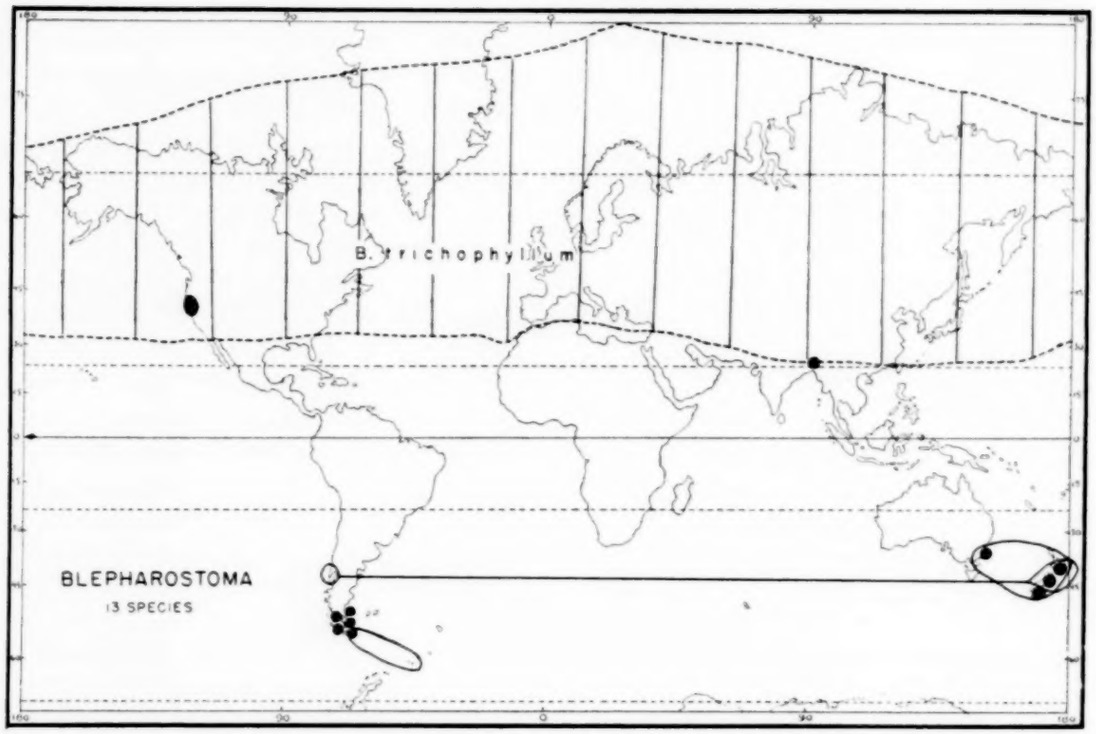

FIG. 5. Map showing the distribution of *Blepharostoma*, a genus showing a bipolar distribution. Most of the species occur in the Southern Hemisphere. One of the northern species is very widespread.

the interpretation of present distribution patterns has been shared by both groups, as well as by other groups of plants, it must be remembered that for the hepatics it has been mostly a matter of the continuance and elaboration of established patterns; moreover, they have been a minor element of the flora, while for the flowering plants it has been a time of internal and external expansion and differentiation as well as of aggression leading to dominance over most of the earth.

The genera disjunct in the Southern Hemisphere fall roughly into three groups, related in a large part to the present climate. They are, namely, a) tropical genera, b) subtropical/tropical-temperate-Antarctic genera, and c) Antarctic genera.

a) Tropical Genera. Dobzhansky (1950) and many before him have commented on the great contrast between the temperate and tropical floras, and have emphasized the luxuriance, powerful growth, and variety and elaborateness of forms in the tropical rain forest. This is equally true for the Hepaticae of the tropics, and is particularly strongly emphasized in the family *Lejeuneaceae*.

Among the liverworts of tropical South America—or elsewhere in the tropics, this family is most characteristic. It is a large family of some 70 genera, which is limited largely to tropical regions of the world, with only an occasional species extending into the North and South Temperate Zones. When one examines the family as a whole, the morphological evidence indicates that it is an old one, and certain characters indicate that the family as now understood is made up of two phyletic lines (the subgroups *Holostipae* —with entire underleaves, and *Schizostipae*—with bifid underleaves), which have been distinct for a long time. The third subgroup, the *Paradoxae*, which may have evolved from the *Schizostipae* line, consists of two additional lines—A, with twice the usual number of underleaves, and B, without underleaves.

TABLE 1. *Distribution of the genera of the Subgroups of the large tropical family,* Lejeuneaceae, *with a total of 70 genera, 55 of them in South America*

	Endemic	Wide	So. Hem.—Amer.—Malay (not Africa)	Amer.—Afr.—Sikkim	Odd	Total
Holostipae	9	12	1	3–4	0	26
Schizostipae	15	16	2	0	1	34
Paradoxae						
A	2	2	0	0	0	4
B	2	3	1	0	0	6
Total	28	33	4	3–4	1	70
	40%	47%	5.7%	5.7%	1.4%	

Distribution of endemics: 14/28 Amer.; 2/28 Afr.; 8/28 Malay; 4/28 Japan.

While this more or less composite family is highly specialized and shows many advanced or simplified characters (through reduction), and much elaboration, there are a surprising number of characters in some of the genera which are definitely of a primitive nature. This is particularly true of many members of the *Holostipae* where one finds undifferentiated or slightly differentiated stems, branching of the *Frullania* type, undivided underleaves, little or only gradual differentiation between leaves and female bracts, and often a three-keeled perianth.

An examination of the distribution pattern of this family (table 1) shows that of the 70 genera, at least 55 occur in South America; of the 70 genera, 28 or 40% are endemics, which in itself might point to the great age of this family. Half the total number of endemics, 14 of the 28, are in South America (including Central

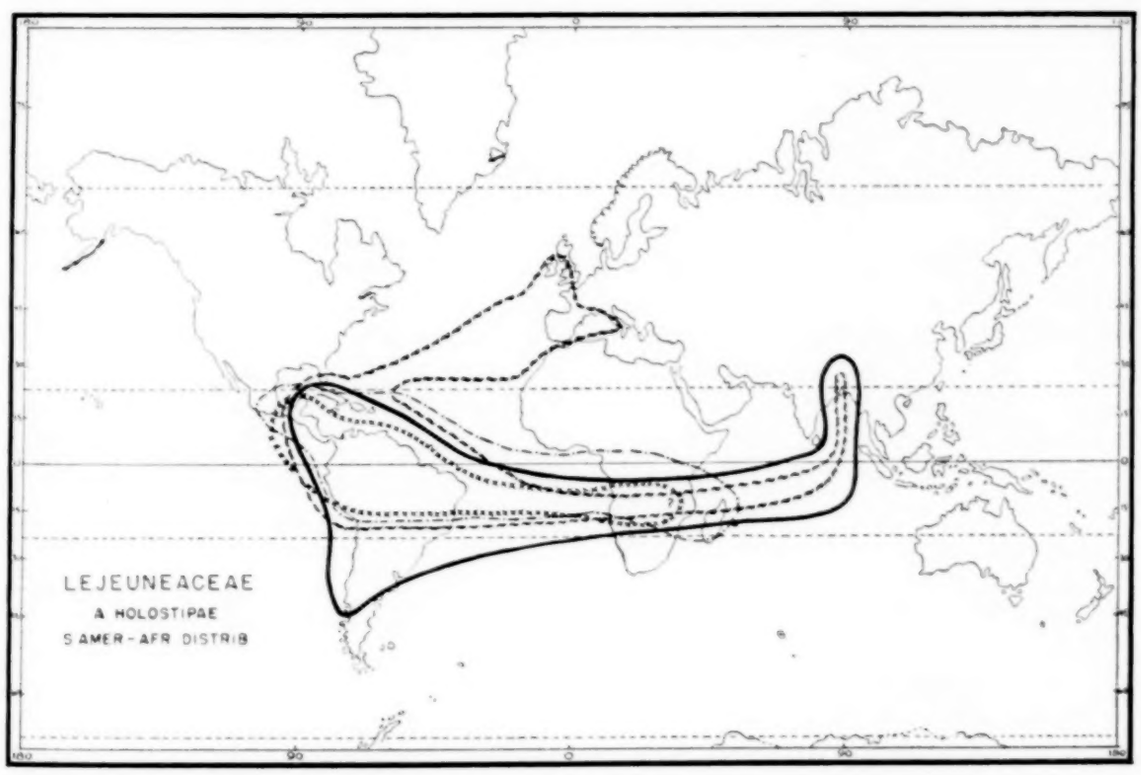

FIG. 6. The distribution patterns of 4 of the genera of the Subgroup *Holostipae,* of the family *Lejeuneaceae.* These 4 genera show many primitive characteristics.

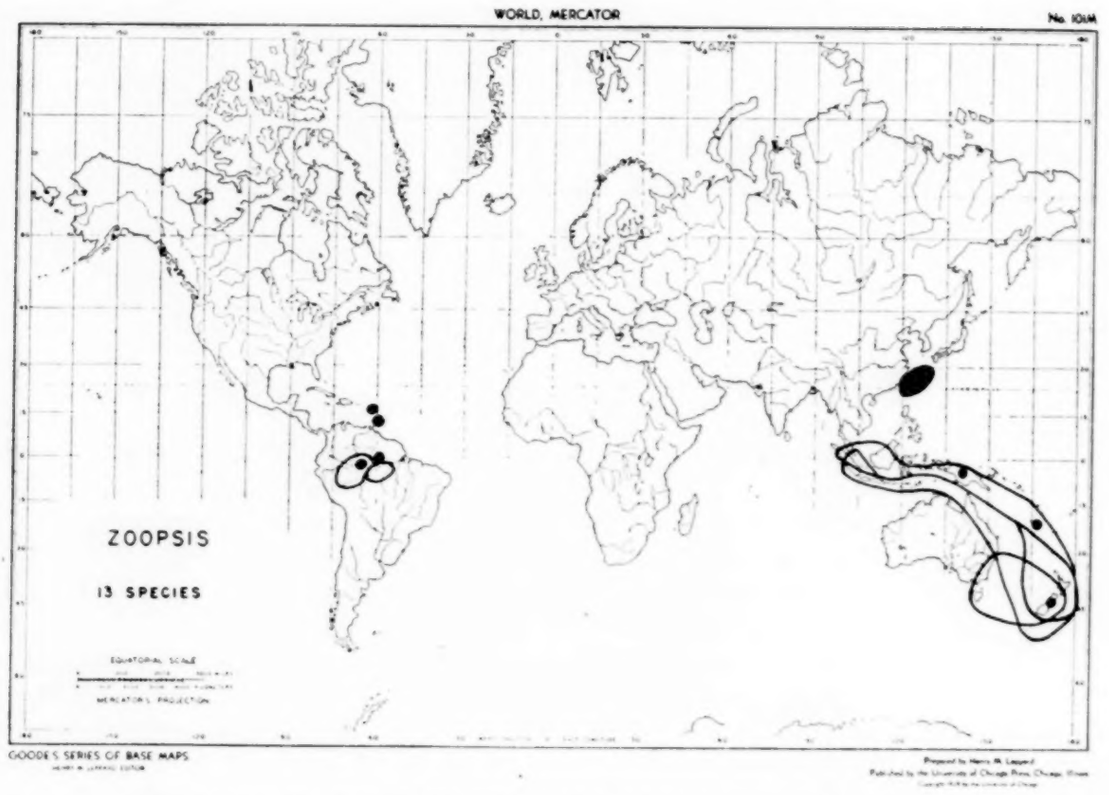

FIG. 7. Map showing the distribution pattern of *Zoopsis*, a genus with a discontinuous distribution in Tropical America, the Malayan Archipelago, Formosa, eastern Australia, New Caledonia and New Zealand.

America and the West Indies). Does this indicate that the South American land mass was the possible center of origin of the *Lejeuneaceae*, or at least that it is the existing area where the family has been present for the longest time?

Nearly half of the genera, 33 of the 70, or 47%, are widespread in the tropics, a truly disjunct distribution in itself. Furthermore, more than half of this number, 19 of the 33, are reported to occur in the Nepal-Sikkim area.

When the *Holostipae*, the group with the most primitive characters, is examined more closely, it is found that in addition to 9 endemic genera (4 of them in South America), 12 genera are widespread (8 of them in the Sikkim area). In addition, there is a group of at least 4 genera which are predominantly in Tropical America but have one or a few species in Africa. Some of these genera also extend into Sikkim. Figure 6 shows the distribution patterns of these latter. They include the following: *Bryopteris*, with about 13 species, 10 of them in tropical America, 2 in tropical Africa,[6] and a species in Nepal; *Marchesinia*, with a similar distribution except for one northern species which has an "Atlantic" distribution in Europe; and *Odontolejeunea*, with about 22 species in South America and Africa. The genus *Peltolejeunea*, with about 5 species may have a similar distribution.

Then there are the *Lejeuneaceae* which occur in tropical America and in Indo-Malaya. *Taeniolejeunea*, with a species common to Japan and Jamaica and about 8 species in the Malayan Archipelago and Japan, is one of these. The data are based on a recent monograph.

Additional tropical genera of other families which show a somewhat similar distribution but are more widespread in

[6] One or both may be identical with American species, fide C. Vanden Berghen, in a personal communication.

the Pacific area include: *Calobryum*, reported from the West Indies and Peru, and southern Japan, New Guinea, Java and New Zealand; *Zoopsis* (fig. 7), in the West Indies and Brazil, and the Malayan Archipelago, Formosa, New Caledonia, eastern Australia and New Zealand; and *Psiloclada*, in Brazil, and the Malayan Archipelago, eastern Australia and New Zealand. All of these genera possess many primitive or simplified characters.

b) Subtropical/tropical—temperate—Antarctic Genera. The genera of this group occupy, for the most part, not only tropical and subtropical but also temperate and cold areas of the Southern Hemisphere. Some of the genera of this group too, also occur in the Sikkim area of India.

In their structural organization most of the genera exhibit characters which are of a primitive nature, and many of them are members of two families, *Ptilidiaceae* and *Lepidoziaceae*, both primitive (Evans, 1939).

Many of the genera are large and have become segregated within themselves into groups or Sections, which differ widely in structure as well as in distribution pattern. Certain sections of a genus are tropical and subtropical or nearly so; other sections are more typically of the temperate regions of South America; while still others are cold temperate and circumpolar. This is illustrated by the genus *Bazzania* (see Fulford, 1946). Because of its large size it might be considered by some to be subcosmopolitan. It is predominantly of the Southern Hemisphere. In South America, at least, the Section *Appendiculatae* is predominantly tropical; the Section *Connatae* is in part tropical and in part occurs in abundance in Patagonia, South Africa and New Zealand; and the Section *Vittatae* is predominantly cold temperate in South America, Africa, and Australia-New Zealand. The Sections also occur on the other land masses of the Southern Hemisphere together with the Section *Fissistipulae*

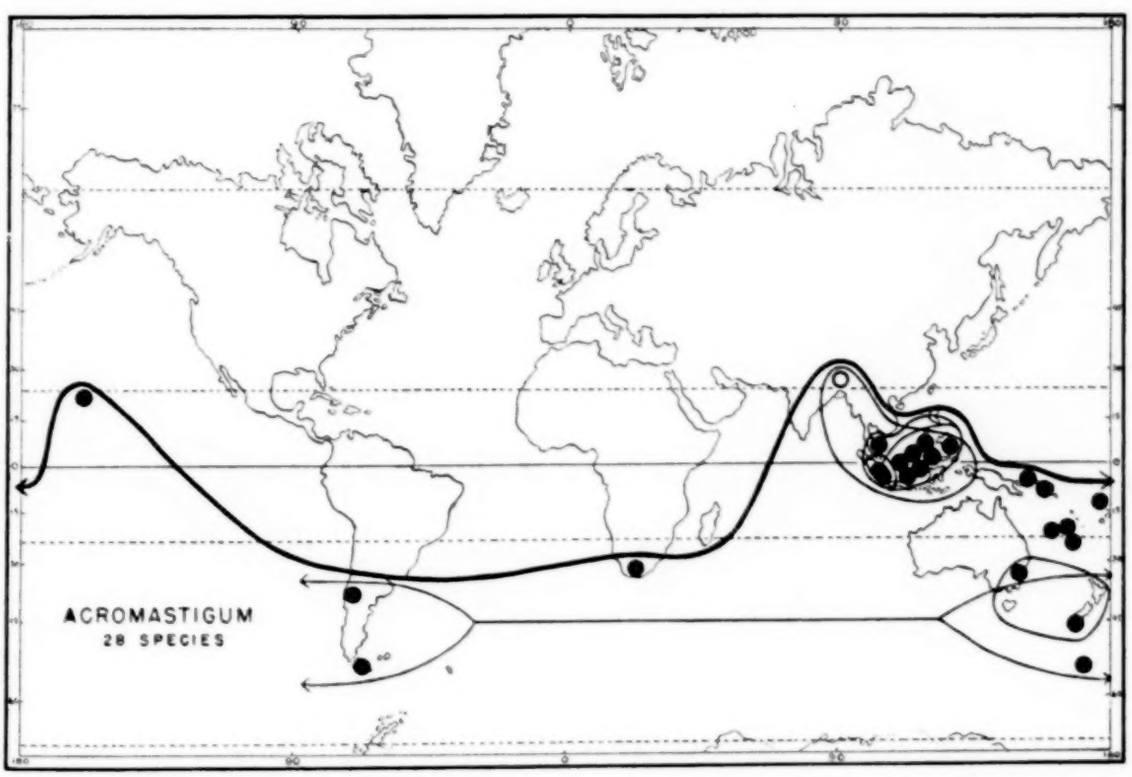

FIG. 8. Map showing the distribution of *Acromastigum*, a genus discontinuous in subtropical/tropical—temperate—Antarctic areas of the Southern Hemisphere. One species is common to South America and the New Zealand-Tasmania area; another which occurs in the Malayan Archipelago is also found in Sikkim. Most of the species are local endemics.

which is absent from South America. A few of the species of this southern genus as well as of many of the other southern tropical and temperate ones, have recently migrated into the Northern Hemisphere. The pattern of distribution of this group is illustrated by the genera below.

The genus *Acromastigum* (fig. 8), monographed by Evans (1934), includes 28 species, one of which occurs in South America (Chile), Australia, Tasmania, New Zealand and the Auckland Islands; another in Tasmania, New Zealand and southeastern Australia; 2 are widespread in the Malayan Archipelago; another in the Malayan Archipelago and with a station in Sikkim; and the rest are local endemics.

The genus *Lepicolea* (fig. 4), which was mentioned earlier, in the discussion of bipolar distribution, is, in all except its isolated northern species, another example of this type of distribution. Some species are restricted to South America, one is common to southern South America and the southern tip of Africa, and others are local or widespread from New Zealand to Japan.

The genera *Lembidium* (fig. 9), with about 10 species, *Balantiopsis* (fig. 10), with about 20 species, and the species of *Blepharostoma* (fig. 5), which occur in the Southern Hemisphere, follow the same pattern of distribution. Another, *Isotachis*, a large genus of some 75 species, has become segregated into Sections in much the same way as the genus *Bazzania*, and its distribution in the Southern Hemisphere is similar. *Symphyomitra* and *Marsupidium* also show this sort of distribution.

These patterns of distribution, which are not unusual in the Southern Hemisphere, follow the pattern shown by Florin (1940) for a number of the living members of the Sections *Dacrycarpus* and *Polypodiopsis* of the genus *Podocarpus*, or the Sections *Eutacta* and *Colymbea* of

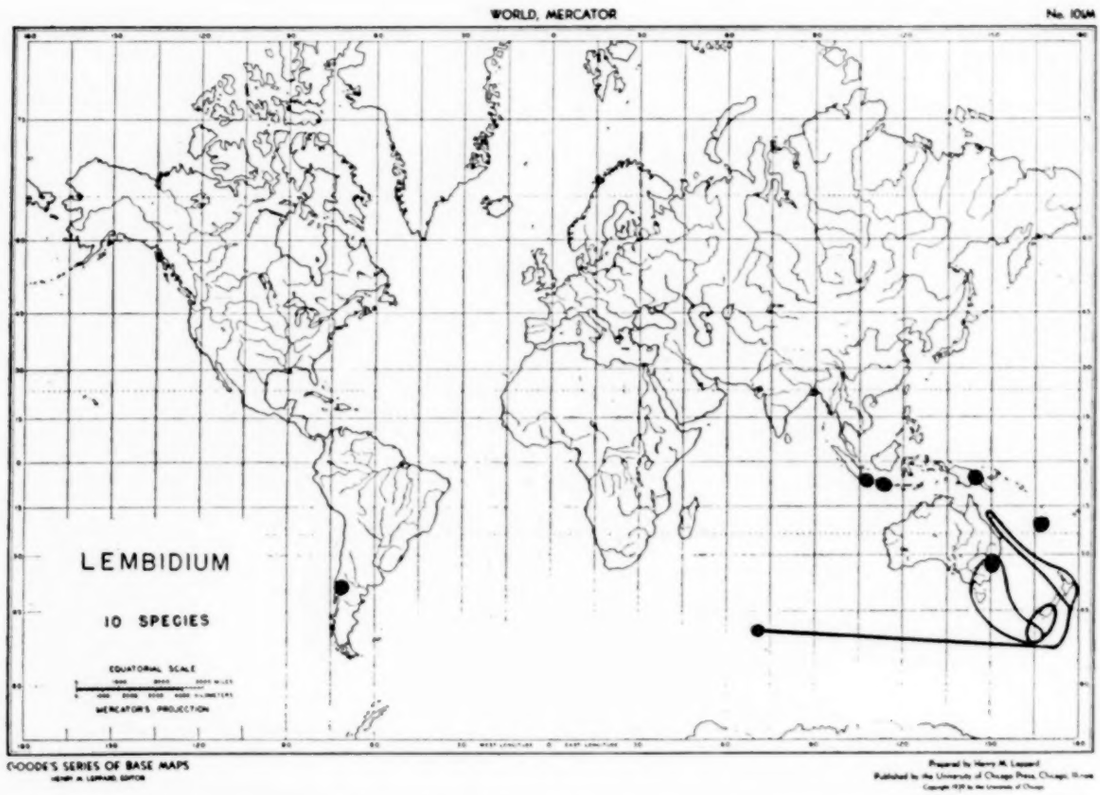

FIG. 9. Map showing the distribution of *Lembidium*, a genus discontinuous in South America, Kerguelen Island, the Malayan Archipelago, New Caledonia, southeastern Australia and New Zealand. Some of the species are rather widely distributed as shown by the solid lines.

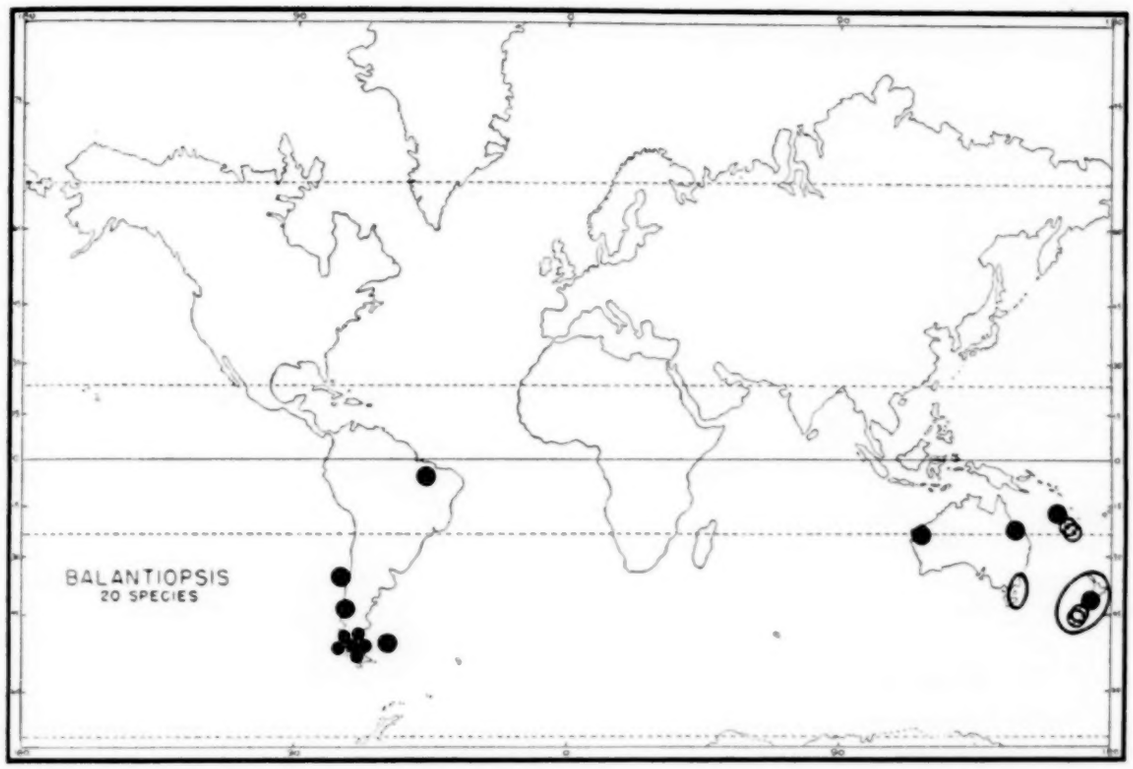

FIG. 10. Map showing the distribution of *Balantiopsis*, a genus discontinuous in South America and Australia—New Caledonia—New Zealand. Most of the species appear to be local.

the genus *Araucaria*, in the Southern Hemisphere. Dr. Florin also had a fossil record of these same groups and the latter indicates that these groups were more abundant and more widespread in the southern floras of Mesozoic and Tertiary age, and at least some of them existed in South America, Antarctica, New Zealand, Tasmania,[7] eastern Australia and peninsular India. The living members represent the distribution patterns of *old groups* of plants.

The Section *Dacrycarpus* of *Podocarpus* now occurs only in southern China and Thailand, Burma, Malayan Archipelago, New Caledonia and New Zealand (fig. 11), while formerly it occurred at least in what is now southeastern Australia, New Zealand, Tasmania[7] southwestern South America and Antarctica, as is indicated in figure 11. The living members of the Section *Polypodiopsis* occur in Melanesia and in two localities in northwestern South America. Fossil records have been found in New Zealand, Tasmania,[7] and in southwestern South America.

In *Araucaria*, the living members of the Section *Eutacta* (fig. 12) are known from the eastern part of the Malayan Archipelago, New Caledonia, and eastern Australia, while the fossil record includes South Africa, India, eastern Australia, New Zealand, Tasmania,[7] southern South America and Antarctica. The Section *Colymbea* (fig. 12) has living members in eastern Australia and the eastern tip of the Malayan Archipelago, and southwestern and eastern South America. The fossil record includes the southeastern tip of Australia, Tasmania, New Zealand, southern South America and Antarctica, and possibly northeastern India.

This study by Dr. Florin indicates that these "old" groups now found in widely separated localities in the Southern Hemisphere were at one time distributed over

[7] Dr. Florin has called my attention to the fact that Tasmania has recently been added to the area included in the fossil record of these groups, fide a personal communication; see also, Selling, O. H. Svensk Bot. Tidskr., **44**(4): 551–561. 1950.

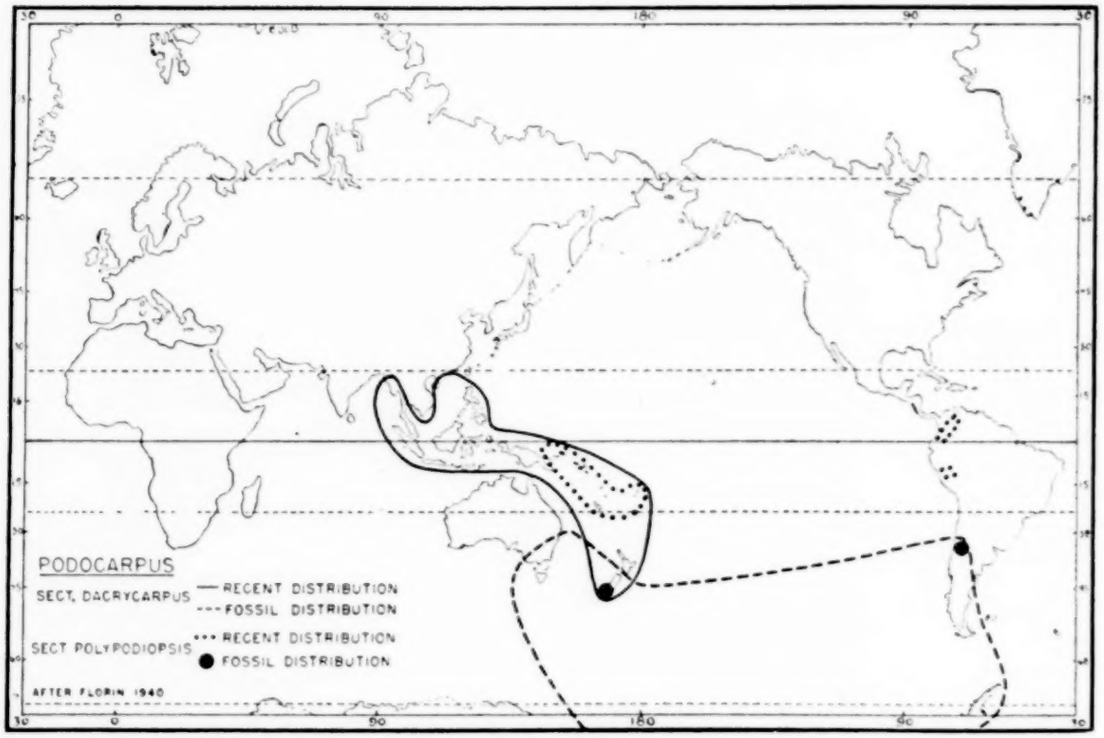

FIG. 11. Map showing the distribution of *Podocarpus*, Sect. *Dacrycarpus*, showing Recent ————, and fossil - - - - - - distribution; Sect. *Polypodiopsis*, showing Recent ....., and fossil ● distribution. (After Florin, 1940.)

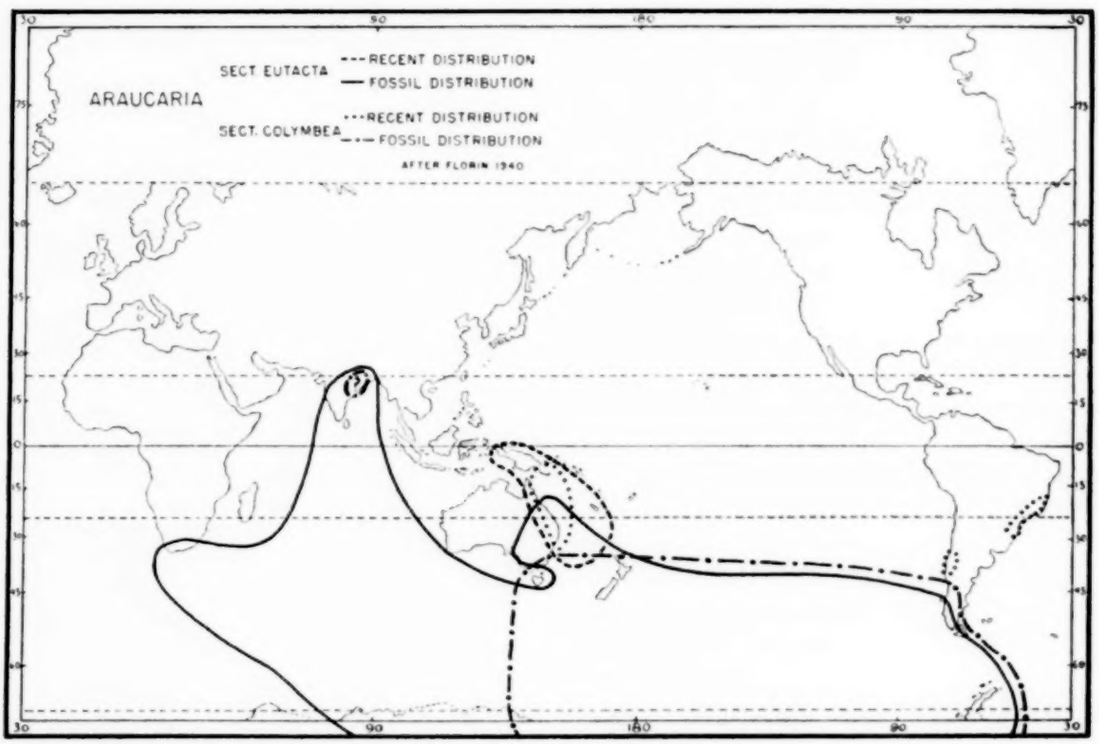

FIG. 12. Map showing the distribution of *Araucaria*, Sect. *Eutacta*, Recent - - - - - -, and fossil ———— distribution; Sect. *Colymbea*, Recent ....., and fossil —·—· distribution of the group. (After Florin, 1940.)

broad areas of that Hemisphere. Some also extended into what is now India. Antarctica was covered by a similar vegetation. It is reasonable to suppose, then, that the genera of hepatics with a distribution similar to that of the living members of the above Sections of *Podocarpus* and *Araucaria* might also be considered to have been widespread over an area which included the present land masses of the Southern Hemisphere and also India and Antarctica. These present disjunct patterns of distribution among the hepatics are remnants of this former widespread distribution. The fact that these genera of Hepaticae which show such distribution belong to primitive families or are simplified members (through a decrease in complexity) of other families and have the characteristics of "old" groups, adds to the weight of this argument.

c) Antarctic Genera. The distribution patterns of these genera are perhaps most striking of all. They are found in southern Chile and/or Patagonia, Falkland Islands, Kerguelen Island, Campbell Island, Auckland Islands, New Zealand, Tasmania, and southeastern Australia. Sometimes they occur in South Africa or in Sikkim.

The subdivision includes the Antarctic type, the South Pacific type (South America-Pacific Islands, New Zealand and/or Australia), and the South Atlantic type (South America, Africa and Madagascar), of discontinuities mentioned by Wulff (1943, pp. 82–91).

The genus *Herpocladium* (fig. 13) is an example of this type. There are 7 species, one common to Patagonia and the Auckland Islands, three on South Atlantic Islands, one on Kerguelen Island, one in Hawaii, and one in Sikkim.

The genus *Lepidolaena* (fig. 14) shows an even more striking distribution. There are about 13 species: four are endemic in southern South America; six are endemic in the New Zealand-Australia area; and three species are common to the southern

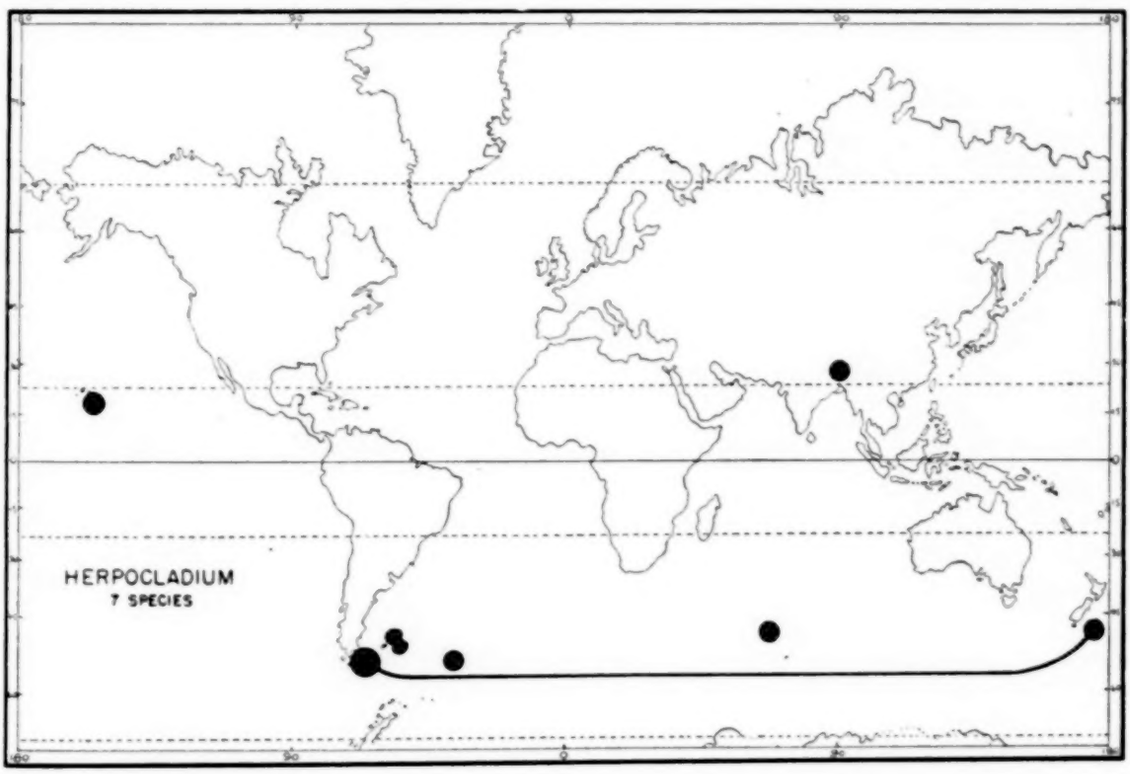

FIG. 13. Map showing the distribution of *Herpocladium*, a genus which, for the most part, is discontinuous in the Antarctic region. One species occurs in Sikkim. One species is common to South America and the Auckland Islands.

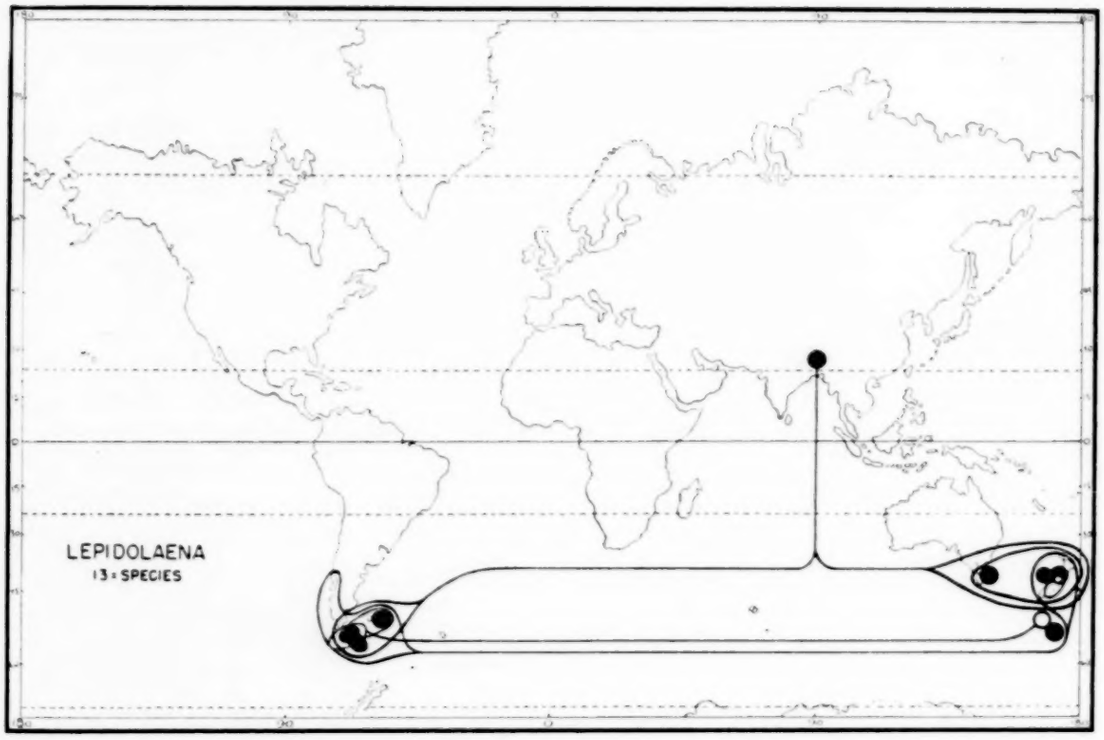

FIG. 14. Map showing the distribution of *Lepidolaena*, a genus discontinuous in the Antarctic region. Three species are common to South America and southeastern Australia—New Zealand, and one of these also occurs in Sikkim.

tip of South America and New Zealand—Tasmania—southeastern Australia, with one of these in South America, New Zealand—southeastern Australia and also in Sikkim. I have examined the latter specimens, collected by Hooker and now in the New York Botanical Garden, and they are correctly determined.

While a number of genera characteristically occupy cold temperate tips of the continents or the islands of the South Pacific, South Atlantic and southern Indian Ocean, both *Herpocladium* and *Lepidolaena* have an even more striking discontinuous distribution, for each has a disjunct species far out of the usual range for the genus, thousands of miles to the north in Sikkim. Are these disjunct genera, too, remnants of a once more widespread distribution at a time when the land configuration was such that a continuous distribution was possible in areas now as widely separated as South America, New Zealand—Australia, and Sikkim? Both genera are members of the same primitive family, *Ptilidiaceae*, to which certain of the Subtropical/tropical—temperate—Antarctic disjuncts described earlier belong.

DISCUSSION

Just what is the significance of such patterns of distribution? To be sure, since these are spore-bearing plants which, in addition, in many instances produce one or another type of gemmae or small vegetative reproductive body, one would naturally suppose that they would be uniformly widespread, and that any problems concerning present distribution certainly would be answered through the ease and rapidity of their dispersal. The present widespread distribution patterns of certain species and genera seem to bear this out.

Yet there are other categories of leafy Hepaticae which are not widespread but, rather, are narrow or broader endemics, or which show a discontinuous or disjunct distribution, often with great dis-

tances intervening. It is these that offer the important clues to the past history of the Hepaticae.

Many, including Domin (1923), Herzog (1926) and Irmscher (1929), have discussed the possibility of an explanation of such discontinuous distribution patterns through long distance spore dispersals via wind, birds, ocean currents, and the like, and have concluded that the answers to this problem are not to be found in such methods of dispersal.

Too, the investigations on the culture of leafy plants and of spores (by Garjeanne, Killian, Buch, Fulford, Geldreich, Schmidt and Fulford, and others) would seem to indicate that certainly in many groups, *Lejeuneaceae* (*Leucolejeunea, Taxilejeunea,* etc.), *Lepidozia, Ptilidium,* etc., the spores and gemmae could, at most, account for spread of the species within adjacent areas only. The survival ability of the spores of the species named above, under the wide variety of culture conditions which were tried, was very low, and this was under the best conditions! The spores, in particular those of the *Lejeuneaceae,* were viable for a short period only, since any drying out, even an exposure to air in the laboratory for less than an hour, killed them. The spores of the *Lejeuneaceae* are green, and to some extent begin their germination while yet in the capsule, so that by the time they are shed, they are really sporelings in an early stage and are extremely delicate.

The spores are not built for travel over long distances, and there appear to be no intermediate stations for genera such as *Lepidolaena* between New Zealand and Sikkim, or New Zealand and Patagonia. Furthermore, the species of this genus apparently have not spread northward even along the Andes from Patagonia, where certainly some suitable habitats must exist.

For the most part, the species of such disjunct genera, apparently no longer very aggressive, have been able to persist unchanged over a long period in limited areas which in themselves have not been subjected to violent or drastic disturbances.

It would seem that in the past there must have been a more widespread distribution and either a different land configuration or some sort of overland migration routes which are no longer present, to account for the similarity in distribution patterns in groups of genera not closely related that are 1) circumpolar in the Antarctic region and are present also in Nepal-Sikkim, or 2) in tropical South America, in tropical Africa and in Sikkim, or 3) in widely separate temperate regions. Since there is no evidence of land connections between South America and Africa since before the Cretaceous and no connection between Africa and India for an even longer time, perhaps these are remnants of a flora which was widespread before these land masses became isolated.

Such distribution patterns are not limited to the leafy Hepaticae but, rather are repeated over and over again in many groups of plants, most of which do not reproduce by spores. These patterns have been pointed out by many, including Cain (1944), Camp (1947), Copeland (1947, pp. 1–10), Domin (1923), Du Rietz (1940, esp. pp. 239–240), Florin (1940), Good (1947), Herzog (1926), Hutchinson (1926, 1944), Irmscher (1922, 1929), Skottsberg (1934, 1936) and Wulff (1943).

Carpentier (1923), Sahni (1926), Seward (1931), Florin (1940), Chaney (1948), Stebbins (1950) and others have given us a survey of the past floras of the Southern Hemisphere based on the evidence from the fossil plant record. Two points are particularly pertinent. In the first place, by Permo-Carboniferous time two distinct floras had become segregated, the one in the Northern Hemisphere, the other in the Southern Hemisphere. The latter area supported a more or less uniform flora which was similar in what is today India, Australia, Africa, Falkland Islands and Antarctica. In the second place, in Jurassic time the flora

of the Southern Hemisphere still showed a widespread uniformity, and fossils of similar aspect have been collected from South America, Falkland Islands, Antarctica, Graham Land, South Africa, Madagascar, New Zealand, Australia, New Caledonia and India. It was distinct from the northern flora, at least in so far as the conifers are concerned. The aspect of the vegetation had changed to that of a modern type and some of the fossil species of *Podocarpus* belong even to the same sections of the genus as do the living South Temperate species (Florin, 1940).

Since that time there has been both an ecological and a geographical segregation of the units, together with some evolutionary change in the plants themselves. These have resulted in the modern distribution patterns of some of the old groups.

Based on what is known of the distribution of the floras, the land relations, and the climates of the past, my interpretations of the history of the genera of the leafy Hepaticae with discontinuous distribution in the Southern Hemisphere is as follows:

The actual disjunction of the widespread tropical genera of the *Lejeuneaceae*, as well as that of the genera limited to tropical South America and Africa but sometimes occurring in Sikkim, the disjunction in genera of other families in the Subtropical/tropical—temperate—Antarctic areas, and that in the Antarctic genera, suggests that the land masses of the Southern Hemisphere were in communication with one another in some manner at times in the past. These lands include South America, Africa, South Atlantic Islands, Antarctica, New Zealand, Australia, Malayan Archipelago and India. Evidence from the studies of fossil floras would seem to place the last possible time of these widespread land connections as the Jurassic Period.

At the latest time when these lands appear to have been in communication, several phyletic lines of leafy hepatics were already present. One of the major ones was the *Lejeuneaceae* line, already segregated into its subgroups and various of its present-day genera. Another was the *Frullaniaceae*, and still others include a number of the phyletic lines with the genera which Evans (1939) has included in the primitive families *Ptilidiaceae* and *Lepidoziaceae*.

Since the fossil evidence from other groups of plants indicates some ecological segregation even during Jurassic time, no doubt the hepatics too had become restricted in their habitats. At any rate, with changing climates, ecological segregation became conspicuous later.

The *Lejeuneaceae* remained in or became adapted to moist tropical climates and have persisted or become limited to areas where such climates exist. The spread of tropical climates to the north and south of the equator preceding or during Eocene time resulted in the spread of a certain few of the species. This accounts for the presence of the few scattered members of tropical genera which we find in the temperate zone today. Such a northern extension is to be seen in figure 6.

The members of many of the other ancient phyletic lines have persisted, for the most part, in the more temperate climate to the south. Let it be remembered that at one period these tropical and temperate floras must have lived as contemporaries under similar conditions. Was it an inability to compete with the tropical forms, or an inability to adapt physiologically to the later tropical habit that caused the so-called temperate forms to disappear from the land that is tropical? Most of these now temperate zone forms also must have occupied Antarctica, for evidence presented by Florin (1940), Skottsberg (1934, 1936), Du Rietz (1940) and others indicates that until rather recently this large continent was forested.

In more recent times Antarctica may easily have served as a "highway bridge" between New Zealand, Australia, South

America, and some of the subantarctic islands; and this may be the explanation for a part of the disjunct patterns found among the plants of the Southern Hemisphere, particularly those of the Temperate region.

But, such an Antarctic "Bridge" is not the *whole* explanation of the patterns of disjunct distribution among (a) the tropical genera, or (b) the subtropical/tropical—temperate—Antarctic, or even (c) the Antarctic genera of leafy Hepaticae, especially for those with a disjunct occurrence in Nepal-Sikkim or perhaps some of those also in Africa. The disjunct patterns, both of the tropical genera and of those of the southern temperate genera, must have come about through the fragmentation of the vegetation at an earlier time, when it was more or less uniform and was very widespread, covering in Jurassic time the land area of the Southern Hemisphere including what is now India.

With the continued isolation or near isolation of the land masses which the remnants inhabited, this aspect of a widespread uniformity of the flora was lost. Some of the species appear to have remained unchanged, some have no doubt disappeared, and new ones have evolved. Without doubt, genera and even families have come into being or have disappeared. The living leafy Hepaticae are thus the end products of these many lines of descent, some old, some more recent. All of them reflect not only their own developmental history and phylogeny, but also something of the history of the vegetation of which they are a part.

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PHYLOGENETIC RELATIONSHIPS OF CERTAIN RACES OF *EUOENOTHERA* FROM MEXICO AND GUATEMALA[1]

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INTRODUCTION

Oenothera has long enjoyed biological fame for its unconventional cytogenetic behavior.[2] In recent years these cytogenetic peculiarities have been effectively utilized in determining phylogenetic relationships in the North American section of the subgenus *Euoenothera* (Cleland, 1935, 1937, 1940, 1949). The present paper is a report of similar phylogenetic studies on races of *Euoenothera* from Central America and Mexico. These races, like the California forms, lack cytogenetic specialization. Although similar to the California races phenotypically, they differ sufficiently to be assigned to a distinct species by Munz (1949). The question therefore arises as to whether this group is to be considered closer to the ancestral line of the North American euoenotheras or whether the California group is more primitive. A cytogenetic analysis of the races from Mexico and Guatemala should throw light upon this problem.

The material from Guatemala was studied for another reason also. It has hitherto been difficult to obtain crosses between the North American euoenotheras and the South American forms. It was hoped that races from Central America might cross readily with both North and South American races and hence serve as bridging forms, which would make it possible to bring all of the euoenotheras into a single cytogenetic system. The Guatemalan material, however, does not cross readily with South American euoenotheras, although it crosses readily with those from North America. Its affinities seem to be definitely North American, and its value as a bridging form is questionable. Further discussion of this phase of the study, therefore, will be omitted from the present paper.

MATERIALS AND METHODS

The new races analyzed in this study are listed in table I. These were hybridized with a series of "standard" races (table II) whose complexes had previously been analyzed genetically and cytologically. Each hybrid combination was identified phenotypically and its chromosome configuration determined. From these configurations the segmental arrangements of the new complexes were worked out. For further information regarding the standard races see Cleland, 1935, 1937; Cleland and Hammond, 1950; Geckler, 1950; Preer, 1950.

The race *Guatemala* actually represents two collections from Guatemala, one from Guatemala City, the other from Chichicastenango. These two collections proved to be phenotypically and segmentally indistinguishable. For this reason, only the strain from Guatemala City, which we have named *Guatemala*, has been used in the present study.

All cytological material was prepared according to the schedule described by Hecht, 1950. Chromosome configurations were determined from pollen mother cells in late diakinesis or metaphase I. Wherever possible, determinations were obtained from at least two plants of each complex combination.

[1] This study was made possible through grants from the Rockefeller Foundation and Indiana University to Dr. Ralph E. Cleland for research in *Oenothera* cytogenetics. The material and facilities used in this study were provided through the courtesy of Dr. Cleland, whose continued interest and guidance throughout the course of the work are gratefully acknowledged.

[2] For a review of *Oenothera* cytogenetics see Cleland, 1936.

TABLE I. *New races included in the present study*

Race	Source	Collector	Year	Chromosome configuration
Chapultepec	Dist. Fed., Mexico	P. A. Munz	1937	7 pairs
Guatemala	Guatemala City, Guatemala	P. Weatherwax	1945	7 pairs
Texmelucan	Puebla, Mexico	P. A. Munz	1937	7 pairs
Toluca	Mexico, Mexico	P. A. Munz	1937	7 pairs
Zimapan	Hidalgo, Mexico	P. A. Munz	1937	7 pairs

DESCRIPTION OF NEW RACES

I. Characters common to all new races:

Leaves of moderate size (largest cauline leaves 8.5–19.5 cm. long, 2–3 cm. wide), light green with a grayish cast, elliptic-lanceolate, acute; surface smooth to very slightly crinkled, strongly wavy; margins entire to obscurely toothed; marginal hairs appressed; surface hairs moderately numerous, fairly short to medium in length, closely appressed; midrib white; pulvinus green.

Stems. Papillae usually absent or indistinct; a strong, felty pubescence.

Habit. Central shoot usually well developed with numerous lateral branches which often reach the same height as the central shoot; no rosette formation when grown in central Indiana.

Bracts moderately to strongly flared, green.

Buds. Cone 2.2–3.5 cm., hypanthium 2.3–3.2 cm., ovary 1–1.5 cm.; cone somewhat angular, tapered, 4–6 mm. thick at base, thick skinned, yellow green to red

TABLE II. *Segmental arrangements of previously determined complexes which are involved in the present analysis*

Complex	Race	Formula for segmental arrangement						
α Birch Tree 1	*Birch Tree 1*	1·2	3·4	5·14	7·10	9·8	11·12	13·6
β Birch Tree 1	*Birch Tree 1*	1·4	3·13	5·7	8·12	9·10	11·6	2·14
α Birch Tree 3	*Birch Tree 3*	1·5	3·13	2·6	7·12	9·14	11·10	4·8
β Birch Tree 3	*Birch Tree 3*	1·4	3·2	5·11	7·10	9·6	8·14	13·12
*[h]blandina**	*blandina*	1·2	3·4	5·6	7·10	9·14	11·12	13·8
α Camas	*Camas*	1·9	3·5	4·6	7·10	2·8	11·14	13·12
β Camas	*Camas*	1·4	3·2	5·10	7·14	9·8	11·12	13·6
curtans	*cockerelli*	1·7	3·4	5·8	2·10	9·11	6·12	13·14
elongans	*cockerelli*	1·4	3·2	5·10	7·6	9·14	11·12	13·8
excellens	*chicaginensis*	1·2	3·4	5·6	7·10	9·8	11·12	13·14
flavens	*suaveolens*	1·4	3·2	5·6	7·8	9·10	11·12	13·14
[h]franciscana Shull	*franciscana* Shull	1·2	3·4	5·6	7·8	9·10	11·12	13·14
gaudens	*r-lamarckiana*	1·2	3·12	5·6	7·11	9·4	8·14	13·10
[h]hookeri de V.	*hookeri* de V.	1·2	3·4	5·6	7·8	9·10	11·12	13·14
α Iowa 2	*Iowa 2*	1·2	3·14	5·8	7·11	9·6	10·12	13·4
β Iowa 2	*Iowa 2*	1·4	3·2	5·10	7·6	9·8	11·13	12·14
α Iowa 6	*Iowa 6*	1·2	3·13	5·12	7·10	9·6	11·8	4·14
β Iowa 6	*Iowa 6*	1·4	3·2	5·7	6·10	9·14	11·12	13·8
[h]Johansen	*Johansen*	1·2	3·4	5·6	7·10	9·8	11·12	13·14
jugens	*shulliana*	1·6	3·2	5·14	7·13	9·8	11·12	4·10
maculans	*shulliana*	1·2	3·8	5·6	7·10	9·12	11·13	4·14
neo-acuens	*grandiflora* de V.	1·13	3·2	5·6	7·10	9·8	11·12	4·14
α Paducah	*Paducah*	1·2	3·4	5·14	7·10	9·8	11·12	13·6
β Paducah	*Paducah*	1·14	3·2	5·9	7·8	6·12	11·10	13·4
punctulans	*chicaginensis*	1·4	3·9	5·2	7·8	6·12	11·10	13·14
truncans	*grandiflora* de V.	1·13	3·7	5·2	4·6	9·14	11·10	8·12
velans	*r-lamarckiana*	1·2	3·4	5·8	7·6	9·10	11·12	13·14

* The superscript "h" (haplo-) indicates that the complex occurs in duplicate in a homozygous race.

with numerous, long, closely appressed hairs; sepal tips 5–6 mm. long, appressed; hypanthium yellow green; ovary gray green; stamens do not reach stigma; petals extend to, or beyond, stigma.

Petals fairly large, 2.5–3.5 cm. wide, 2–3 cm. long.

Flowers 4.5–5.5 cm. in diameter.

Fruit thick at base.

Height as grown, 98–132 cm.

II. Characters distinguishing individual races:

Chapultepec: Stems with very deep red basal color which masks tip and papillae color; papillae, if present, indistinct; bud cone red; fruit with longitudinal red bands at corners.

Guatemala: Leaves smaller than in other races in this collection (typical lower cauline leaf 8.5 × 2 cm.); stems lacking basal color; tips below bracts very slightly red late in the season; stem hairs lacking except for the strong, felty pubescence; papillae absent; habit distinctive in that the lowest lateral branches arise from the central shoot several inches above the ground. Cone shorter and thinner than in other races here included, yellow green; stigma characteristically protrudes from the bud before the flower opens; petals and flowers smaller than in other races of this collection.

Texmelucan: Stems with a moderate basal color; tips below bracts green; bud cone reddened along sutures.

Toluca: Stems with a slight to moderate basal color; tips green, bud cone yellow green.

Zimapan: Stems with a strong red basal color, but less pronounced than in *Chapultepec;* tips red, papillae red; bud cone red; ovary with red papillae.

Hybridization

The crosses obtained by hybridizing Guatemalan and Mexican races with the standard races are listed in table III. In general such crosses were highly successful and ample seed was obtained. With very few exceptions germination was uniformly high and the hybrid seedlings were vigorous. The complex combinations ^{h}*Guatemala·curvans* (*Guatemala* × *muricata*), ^{h}*Chapultepec·curvans* (*Chapultepec* × *muricata*) and ^{h}*Guatemala·maculans* (*Guatemala* × *shulliana*) failed to survive, however, because of plastid difficulties. In addition, the following complex combinations showed varying degrees of chlorosis: *flavens·*^{h}*Texmelucan*, *αCamas·*^{h}*Texmelucan*, *gaudens·*^{h}*Texmelucan*, *flavens·*^{h}*Toluca*, *gaudens·*^{h}*Toluca*, and ^{h}*Chapultepec·αPaducah;* these combinations reached maturity, however, in spite of chlorosis."

No attempt was made to carry out a genetic analysis of specific characters shown by these races. Since all the races are homozygous (with respect to chromosomal end arrangement), the phenotypic characters produced by each complex are those reported in the description of the race in which it occurs. The race *Guatemala*, it will be noted, lacks red pigmentation other than a slight tip color when the plants are mature. Evidence from certain hybrids with *Guatemala* indicates, however, that ^{h}*Guatemala* carries a factor for red pigmentation which is ordinarily suppressed in the race itself and in most hybrid combinations. In a few cases, e.g., ^{h}*Guatemala·*^{h}*Alabama*, red papillae, basal color, and cones are shown, even though ^{h}*Alabama* lacks a factor for red pigmentation. The latter complex is presumed to carry a gene preventing the action of the suppressor of color which appears to be present in ^{h}*Guatemala*. Additional crosses are being made to analyze the situation more fully.

Cytological Analysis

To illustrate the manner in which the segmental arrangement of a complex can be derived, the reasoning used to determine the segmental arrangement of ^{h}*Guatemala* will be given. The segmental arrangements of the other complexes (table

TABLE III. *Newly determined chromosome configurations*

Cross	Complex combination	Chromosome configuration
Birch Tree 3 × *Texmelucan*	*α Birch Tree 3* · *ʰTexmelucan*	⊙[1] 8, ⊙ 4, 1 pair
blandina ×	*ʰblandina* · *ʰTexmelucan*	⊙ 4, 5 pairs
× *Toluca*	*ʰblandina* · *ʰToluca*	⊙ 4, 5 pairs
× *Zimapan*	*ʰblandina* · *ʰZimapan*	⊙ 4, 5 pairs
Camas × *Guatemala*	*α Camas* · *ʰGuatemala*	⊙ 10, ⊙ 4
Chapultepec × *Birch Tree 1*	*ʰChapultepec* · *α Birch Tree 1*	⊙ 6, ⊙ 4, 2 pairs
×	*ʰChapultepec* · *β Birch Tree 1*	⊙ 12, 1 pair
× *Birch Tree 3*	*ʰChapultepec* · *α Birch Tree 3*	⊙ 8, ⊙ 4, 1 pair
	ʰChapultepec · *β Birch Tree 3*	⊙ 8, 3 pairs
× *blandina*	*ʰChapultepec* · *ʰblandina*	⊙ 4, 5 pairs
× *Camas*	*ʰChapultepec* · *β Camas*	⊙ 8, 3 pairs
× *chicaginensis*	*ʰChapultepec* · *punctulans*	⊙ 12, 1 pair
× *cockerelli*	*ʰChapultepec* · *elongans*	⊙ 4, 5 pairs
× *franciscana* S.	*ʰChapultepec* · *ʰfranciscana* Shull	⊙ 6, ⊙ 4, 2 pairs
× *grandiflora*	*ʰChapultepec* · *neo-acuens*	⊙ 6, 4 pairs
	ʰChapultepec · *truncans*	⊙ 12, 1 pair
× *Johansen*	*ʰChapultepec* · *ʰJohansen*	⊙ 4, ⊙ 4, 3 pairs
× *Paducah*	*ʰChapultepec* · *α Paducah*	⊙ 6, ⊙ 4, 2 pairs
chicaginensis × *Zimapan*	*excellens* · *ʰZimapan*	⊙ 4, ⊙ 4, 3 pairs
cockerelli × *Texmelucan*	*curtans* · *ʰTexmelucan*	⊙ 8, ⊙ 6
× *Zimapan*	*curtans* · *ʰZimapan*	⊙ 8, ⊙ 6
	elongans · *ʰZimapan*	⊙ 4, 5 pairs
franciscana Sh. × *Texmelucan*	*ʰfranciscana* Sh. · *ʰTexmelucan*	⊙ 6, ⊙ 4, 2 pairs
× *Zimapan*	*ʰfranciscana* Sh. · *ʰZimapan*	⊙ 6, ⊙ 4, 2 pairs
grandiflora × *Zimapan*	*neo-acuens* · *ʰZimapan*	⊙ 6, 4 pairs
	truncans · *ʰZimapan*	⊙ 12, 1 pair
Guatemala × *Camas*	*ʰGuatemala* · *β Camas*	⊙ 12, 1 pair
× *Chapultepec*	*ʰGuatemala* · *ʰChapultepec*	⊙ 6, ⊙ 6, 1 pair
× *cockerelli*	*ʰGuatemala* · *elongans*	⊙ 12, 1 pair
× *grandiflora*	*ʰGuatemala* · *neo-acuens*	⊙ 8, ⊙ 4, 1 pair
	ʰGuatemala · *truncans*	⊙ 8, ⊙ 6
× *hookeri*	*ʰGuatemala* · *ʰhookeri*	⊙ 8, 3 pairs
× *Iowa 2*	*ʰGuatemala* · *β Iowa 2*	⊙ 10, ⊙ 4
× *Iowa 6*	*ʰGuatemala* · *β Iowa 6*	⊙ 12, 1 pair
× *shulliana*	*ʰGuatemala* · *jugens*	⊙ 12, 1 pair
× *Texmelucan*	*ʰGuatemala* · *ʰTexmelucan*	⊙ 6, ⊙ 6, 1 pair
× *Toluca*	*ʰGuatemala* · *ʰToluca*	⊙ 6, ⊙ 6, 1 pair
× *Zimapan*	*ʰGuatemala* · *ʰZimapan*	⊙ 6, ⊙ 6, 1 pair
Iowa 2 × *Guatemala*	*α Iowa 2* · *ʰGuatemala*	⊙ 8, ⊙ 4, 1 pair
Johansen × *Guatemala*	*ʰJohansen* · *ʰGuatemala*	⊙ 4, ⊙ 4, 3 pairs
× *Texmelucan*	*ʰJohansen* · *ʰTexmelucan*	⊙ 4, ⊙ 4, 3 pairs
× *Zimapan*	*ʰJohansen* · *ʰZimapan*	⊙ 4, ⊙ 4, 3 pairs
r-lamarckiana × *Texmelucan*	*gaudens* · *ʰTexmelucan*	⊙ 12, 1 pair
	velans · *ʰTexmelucan*	⊙ 8, ⊙ 4, 1 pair
× *Zimapan*	*gaudens* · *ʰZimapan*	⊙ 12, 1 pair
suaveolens × *Texmelucan*	*flavens* · *ʰTexmelucan*	⊙ 6, 4 pairs
× *Toluca*	*flavens* · *ʰToluca*	⊙ 6, 4 pairs
Texmelucan × *chicaginensis*	*ʰTexmelucan* · *punctulans*	⊙ 12, 1 pair
× *hookeri*	*ʰTexmelucan* · *ʰhookeri*	⊙ 6, ⊙ 4, 2 pairs
Toluca × *Chapultepec*	*ʰToluca* · *ʰChapultepec*	7 pairs
× *chicaginensis*	*ʰToluca* · *punctulans*	⊙ 12, 1 pair
× *Guatemala*	*ʰToluca* · *ʰGuatemala*	⊙ 6, ⊙ 6, 1 pair
× *hookeri*	*ʰToluca* · *ʰhookeri*	⊙ 6, ⊙ 4, 2 pairs
Zimapan × *Camas*	*ʰZimapan* · *β Camas*	⊙ 8, 3 pairs
× *Paducah*	*ʰZimapan* · *β Paducah*	⊙ 12, 1 pair

[1] The symbol "⊙" means "a circle of"; thus, for example, "⊙ 14" means a circle of fourteen chromosomes.

TABLE IV. *Segmental arrangements of complexes in euoenotheras occurring in Mexico and Guatemala*

Complex	Segmental arrangement							Designation
hGuatemala	1·2	3·10	5·9	7·4	6·8	11·12	13·14	G
hChapultepec	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
hTexmelucan	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
hToluca	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
hZimapan	1·4	3·2	5·6	7·10	9·14	11·12	13·8	M
Most common arrangement encountered among races of *Oe. hookeri:*								
	1·2	3·4	5·6	7·10	9·8	11·12	13·14	H

IV) have been derived through similar reasoning, utilizing the cytological data presented in Table III.

hGuatemala

Gives ⊙[3] 12, 1 pair, with *elongans;* it cannot have any of the following *elongans* chromosomes:

1·4, 3·2, 5·10, 7·6 (Gives ⊙ 10, ⊙ 4 with *βIowa 2,* which has these chromosomes)

9·14 (Gives ⊙ 8, ⊙ 6 with *truncans,* which has 9·14)

The pair with *elongans* must, therefore, result from the presence of either 11·12 or 13·8.

Assume that it has 13·8. Gives ⊙ 4, ⊙ 4, 3 pairs, with h*Johansen;* in this combination one ⊙ 4 must include 13·8 of h*Guatemala,* and, therefore, 9·8 and 13·14 of h*Johansen.* h*Guatemala* must have 9·14 in order to complete the circle. This is impossible, since h*Guatemala* cannot have 9·14, as shown above. Therefore, it cannot have 13·8 and must have 11·12.

Gives ⊙ 8, ⊙ 4, 1 pair, with *neo-acuens.* The pair in this combination must result from the presence of 11·12. It cannot, therefore, have 5·6. Gives ⊙ 8, 3 pairs, with h*hookeri* and ⊙ 4, ⊙ 4, 3 pairs, with h*Johansen.* Therefore, in the combination with h*Johansen,* 7·10 must be in one ⊙ 4 and 9·8 in the other. The 5·6 of h*Johansen* must also be in one of these circles. Hence, the circle which includes 5·6 must be one of the following:

(1) 5·6 — 6·9 — 9·8 — 8·5

(2) 5·6 — 6·10 — 10·7 — 7·5

(3) 5·6 — 6·7 — 7·10 — 10·5

(4) 5·6 — 6·8 — 8·9 — 9·5

(1) requires that h*Guatemala* have 5·8 and 9·6; if this were so, it would give at least two pairs with *αIowa 2.* The observed configuration shows only one pair. (1) is thus eliminated.

(2) requires that h*Guatemala* have 6·10. If it had 6·10, it would give at least two pairs with *βIowa 6.* Hence, (2) is eliminated.

(3) requires that h*Guatemala* have 5·10. It cannot have 5·10, since it gives ⊙ 10, ⊙ 4, with *βIowa 2,* which has 5·10. Hence, (3) is eliminated.

(4) cannot be eliminated. Therefore, h*Guatemala* must have 6·8 and 5·9.

Gives ⊙ 12, 1 pair, with *punctulans.* It cannot have any of the following *punctulans* chromosomes:

1·4 (As shown above)

11·10 (Gives ⊙ 8, ⊙ 6, with *truncans,* which has 11·10)

6·12, 7·8 (Since it has 6·8)

5·2, 3·9 (Since it has 5·9)

[3] The symbol "⊙" means "a circle of"; thus, for example, "⊙ 14" means a circle of fourteen chromosomes.

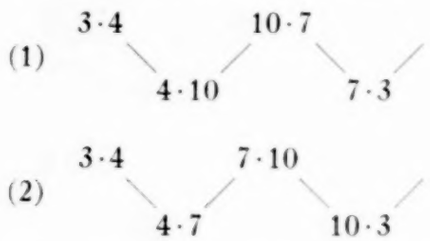
The pair with *punctulans* must, therefore, result from the presence of 13·14.

Gives ⊙ 8, ⊙ 4, 1 pair, with *αIowa 2*. It cannot have any of the following *αIowa 2* chromosomes:

5·8, 9·6 (Since it has 5·9 and 6·8)
7·11, 10·12 (Since it has 11·12)
3·14, 13·4 (Since it has 13·14)

Therefore, the pair in this combination must result from the presence of 1·2.

Gives ⊙ 4, ⊙ 4, 3 pairs, with ^{h}*Johansen*. The three pairs result from the presence of 1·2, 11·12, and 13·14. One ⊙ 4 includes 5·6 and 9·8 of ^{h}*Johansen* and 6·8 and 5·9 of ^{h}*Guatemala*. The remaining circle must be one of the following:



^{h}*Guatemala* cannot have 3·7, since it gives ⊙ 8, ⊙ 6, with *truncans*, which has 3·7. Therefore, (1) is eliminated, and ^{h}*Guatemala* must have 3·10 and 7·4. Thus,

^{h}*Guatemala* = 1·2 3·10 5·9
7·4 6·8 11·12 13·14

This formula gives the correct configuration with all the complexes with which ^{h}*Guatemala* has been combined, including those mentioned above as well as *jugens* (⊙ 12, 1 pair), *αCamas* (⊙ 10, ⊙ 4), and *βCamas* (⊙ 12, 1 pair).

Discussion

Munz (1949) has recently published a taxonomic treatment of the large flowered forms of the subgenus *Euoenothera* which occur throughout southwestern North America and Mexico. According to this treatment, the forms which have been analyzed in the present study belong to *Oe. elata*. Morphologically, *Oe. elata* shows a strong affinity to *Oe. hookeri* which includes the forms occurring in northern Mexico and California. In fact, Munz, in speaking of *Oe. elata*, states, "It is questionably distinct from the *hookeri* assemblage from farther north." Both of these species show similar cytogenetic features, namely, seven pairs of chromosomes at meiosis, the absence of lethals, and open pollination.

On the other hand, *Oe. elata* possesses certain characters which distinguish it from *Oe. hookeri*. *Oe. elata* has thicker fruits, heavier buds, shorter styles, and broader leaves which are often stiff and wavy. Moreover, the results of the present analysis show that the two segmental arrangements found among the races of *Oe. elata* are in each case two interchanges removed from the arrangement which is most commonly encountered among the *hookeri* group. The occurrence of distinctive segmental arrangements, therefore, also argues for the validity of these two species.

The *hookeri* group has in the past been considered primitive among North American euoenotheras. The presence of paired chromosomes at meiosis, freedom from lethals, open pollination, all of which characterize *Oe. hookeri*, are considered to be primitive characters. A further indication that the California races are primitive has been shown by Cleland (1949). With 14 pairing ends and 7 chromosomes in a genome, it is possible to have 91 different kinds of chromosomes with respect to the association of pairing ends. If the frequencies of the different kinds of chromosomes in populations of North American euoenotheras are plotted, seven peaks are obtained which coincide with the seven chromosomes which are found in most of the *Oe. hookeri* races. The wide distribution of these chromosomes which have escaped interchange is good evidence that the *hookeri* arrangement is the ancestral type.

Recognition of *Oe. elata* as a group distinct from *Oe. hookeri* in respect to morphology as well as segmental arrangement raises the question as to the position of *Oe. elata* in the phylogeny of the

subgenus. *Oe. elata*, like *Oe. hookeri*, possesses paired chromosomes, lacks lethals, and is open pollinated. On the other hand, it is interesting to note that most of the chromosomes which characterize the *elata* segmental arrangements (e.g. 9·14, 5·9, 13·8, 3·10, 6·8) do not occur with any appreciable frequency among the populations of North American euoenotheras. *Oe. elata*, therefore, cannot be considered ancestral to the North American forms.

The two *elata* arrangements, M and G (table IV), are a minimum of four interchanges removed from each other. Each, however, is only two interchanges distant from the *hookeri* arrangement. In the evolution of these races it seems unlikely that one has been derived directly from the other, since this would involve, in two forms phenotypically very similar, at least four interchanges. According to a more plausible hypothesis the M and G arrangements have arisen from a common ancestral type, namely the *hookeri* arrangement. In the case of each of the *elata* arrangements two different interchanges are involved, but this is not contrary to expectation. There is no evidence that interchanges involving certain chromosomes occur preferentially (Oehlkers and Linnert, 1949). Thus, if an ancestral arrangement undergoes interchanges at various times during its historical existence, one might expect to have produced a group of forms each of which is the result of a different series of interchanges. *Oe. hookeri*, therefore, appears to be ancestral for the Mexican and Central American races of *Oe. elata* as well as for the North American forms of the subgenus.

In the light of the relationships indicated by the segmental arrangements of these forms it is of interest to consider their geographical distribution. According to Munz (1949) *Oe. elata* ranges through the highlands of central Mexico as well as the highlands of Guatemala, although collections from the latter area are few. *Oe. hookeri* extends from northern Mexico into California and the neighboring states. These two closely related species thus occupy adjacent geographical areas. If we accept the hypothesis that *Oe. elata* was derived from *Oe. hookeri* or an essentially similar ancestral type, the latter must have extended throughout Central America, Mexico, and the southwestern United States before *Oe. elata* became differentiated. Since *Oe. hookeri* and *Oe. elata* are at present still completely interfertile, the latter must have become differentiated through some type of isolation. Presumably this isolation was achieved toward northern Mexico by the climatic changes which occurred in this area in past geological periods. That such changes have occurred is well established, although there is some dispute as to when they took place. Epling (Dobzhansky and Epling, 1944) has reviewed evidence bearing upon climatic changes in the entire southwestern and Mexican region and concludes that the trend toward greater aridity began during the Oligocene; by the end of this period the arid vegetation of the north Mexican plateau had appeared and the climate since that time had remained essentially as it is today. Mayr (1945) disputes these conclusions, maintaining that humid cycles occurred in this region during the Pleistocene. Munz (1949) points out that the oenotheras in the Southwest grow along streams and irrigation ditches and that they cannot be considered members of an arid flora. With the development of an arid climate, therefore, the original *hookeri* or *hookeri*-like population may have been restricted in distribution with populations limited in size and confined to ecologically suitable habitats. The tendency for the originally widespread population to be broken into smaller units could readily have resulted in the development of new forms as localized races in different parts of the entire area.

It is hoped that additional material from this area can be obtained for cytological analysis. Field studies dealing with distribution and ecology of the forms

in this area will also be essential to substantiate the tentative conclusions which are outlined above.

In conclusion, it is of interest to call attention to two points revealed by this study which have a general significance in the cytogenetic approach to problems of phylogeny in *Euoenothera*. It will be noted that races of *Oe. elata* may be as many as four interchanges removed from each other and yet show close morphological similarity. Thus phenotypic changes do not necessarily parallel segmental interchanges in every case. This emphasizes the necessity of correlating cytogenetic evidence with all other available facts, allowing no single type of evidence to serve as an absolute index of phylogeny.

Secondly, these two groups of races illustrate how, with few but divergent interchanges, segmental arrangements can arise which differ sufficiently to produce very nearly a complete translocation heterozygote upon hybridization. Hybrids between Guatemala and any of the other *Oe. elata* races show at meiosis ⊙ 6, ⊙ 6, 1 pair. If two such populations which have undergone divergent interchanges come into contact, translocation heterozygotes will occur. If a system of balanced lethals develops concurrently, a true breeding heterozygote is produced. *Oe. elata* thus represents an early stage in an evolutionary sequence which may ultimately lead to the development of true breeding complex heterozygotes similar to those occurring among the North American euoenotheras.

Summary

1. A group of races of *Euoenothera* from central Mexico and Guatemala is described. These races belong to the species, *Oe. elata*.

2. These races possess all-pairing chromosomes. The segmental arrangements of their complexes have been determined.

3. Two segmental arrangements occur in these races, both of which indicate a close relationship to *Oe. hookeri*.

4. The nature of the relationship between *Oe. elata* and *hookeri* is discussed. Available evidence supports the earlier conclusion that *Oe. hookeri* is the primitive group among the North American euoenotheras. *Oe. elata* also appears to have been derived from *Oe. hookeri*, or a similar ancestral type.

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STUDIES OF VARIATION IN THE WEED GENUS *PHYTOLACCA*. II. LATITUDINALLY ADAPTED VARIANTS WITHIN A NORTH AMERICAN SPECIES

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INTRODUCTION

The preceding paper of this series considered a group of *Phytolacca* populations in tropical America, where active hybridization between quite divergent species has produced extraordinary morphological variability. The present paper considers a more subtle kind of variation found within the single species *P. americana* L. (= *P. decandra* L.), commonly called poke. This species, a native of the eastern United States, is almost completely isolated from other members of its genus; it shows no traces of hybridization except in some Gulf Coast colonies which are to be discussed in the succeeding paper of this series.

Poke is strikingly uniform morphologically throughout most of its range. Comparisons of herbarium specimens, even if drawn from widely separated areas, ordinarily show only the kind of slight quantitative differences which might be attributed simply to varying environmental conditions. Such flat homogeneity is remarkable in view of the wide range of the species, which extends from the Atlantic Coast to the Great Plains and from southeastern Canada to the Rio Grande valley and the Gulf of Mexico. Considering the north-south extent alone, it is apparent that the species must contend with very diverse climatic situations. Its range through more than 20° of latitude includes strongly contrasting day lengths and light intensities. Moreover, though poke has hardy perennial roots, its shoots are extremely sensitive to frost. The northernmost colonies must complete growth and seed production within a frost-free period of less than five months, while the southernmost colonies, living in a zone where years may pass without frost, continue to bloom and fruit through the entire year.

Adaptation of a single species to such diverse environments might be expected to involve evolution of genetically different strains. To explore the possibility that some of the subtle morphological variations in poke are genetically fixed, rather than the direct result of environmental effects, an experimental planting was made in which poke plants derived from different latitudes were grown together under uniform conditions.

NATURE OF THE EXPERIMENT

Seed collected from colonies near Madison, Wisconsin, and Austin, Texas, were planted in a greenhouse at Washington University on December 12, 1946. A uniform, unsterilized light soil mixture was used as a seedbed and for later potting. The Wisconsin seed began germinating in early January, the Texas seed in mid-January. Germination was very uneven; seeds of both lots continued to germinate over a period of more than four months. Only plants which came up between January 15 and February 15 were used for subsequent observations.

In the greenhouse, plants were repotted frequently in a partially successful attempt to keep ahead of the rapid downward growth of the tap roots. In late May both lots were transplanted to a fertile but rather heavy clay loam soil in an outdoor plot in the Missouri Botanical Garden. Plants were spaced about three feet apart and the two lots were interspersed to equalize the effects of any possible edaphic differences. The plot was kept free from other weeds through June, but received no further care during the rest of the summer. Rainfall was heavy

in Saint Louis in June but was below average for the rest of the growing season. July and August were especially dry, with only about a third of the normal rainfall.

A few plants from Missouri seed collected locally were grown under the same conditions and served for non-quantitative comparisons.

Observed Differences

One of the most striking contrasts between the Wisconsin and Texas plants was the universal healthiness of the latter and the high mortality of the former. Within a few days, previously normal Wisconsin plants repeatedly developed heavy red pigmentation, wilted and died. No affected plants recovered. A root parasite was probably responsible, since there was no indication of contagion between adjacent plants and healthy plants were killed when transplanted to soil in which another had died. About 10 per cent of the Wisconsin plants died in the greenhouse and 75 per cent of the survivors died in the outdoor plot during the summer. No Texas plants died either in the greenhouse or outdoors in the course of the experiment. The decreased population size of the Texas group in the September data (fig. 1) resulted from deliberate reduction in numbers at the time of transplanting to the field plot.

The differential mortality of the two lots precluded the original plan of growing and comparing a large and equal population of each. Nevertheless, the available samples provided apparently significant contrasts in many characters. Most of the observed contrasts are summarized graphically in figure 1.

Time of flowering and fruiting. The Wisconsin plants began to bloom more than a month before the Texas plants. Many had developed three or four inflorescences with flowers already open and a few had set seed before the first inflorescences were initiated in the Texas lot. In the fall the Wisconsin lot was conspicuously earlier than the Texas lot in ripening of berries.

Size and habit. From the outset the Wisconsin plants were noticeably smaller in total height, length of branches, and size of leaves and roots. In spite of the size contrasts, the number of nodes and internodes was almost the same in both lots. The habit contrasts are even more striking than the size differences. Figure 2 shows photographs on the same scale of randomly chosen individuals of both strains in late September. The trailing habit of the Wisconsin plants was accompanied by remarkably slender stems and branches, although the number of rings of vascular bundles was essentially the same in both lots.

Branching pattern. Both strains shared the characteristic branching pattern of the species, with each axis terminated by an inflorescence, below which axillary lateral branches arose, which in turn bore terminal inflorescences and axillary branches. This process was repeated over and over until the mature plants bore branches of the tenth or higher order. Although the Wisconsin and Texas plants averaged about the same in the maximum order of branching attained, the Wisconsin lot was much more variable. In both strains the first axillary branch below the inflorescence developed more rapidly than the second, but in the Wisconsin plants the advantage of the first branch was especially great; it usually flowered and bore subsidiary flowering branches before the second branch flowered. The contrast is shown in the graph of terminal branching ratio. This ratio was computed by locating the outermost inflorescence subtended by two axillary branches and then comparing the number of inflorescences on the first branch to the number on the second.

Leaf shape. There is no strong difference in leaf shape between the two strains. Length-width ratios of 100 leaves from each lot were obtained by measuring the 20 outermost leaves on five randomly selected plants. The overall me-

dians of the two lots were found to be almost identical. The medians of the three largest and of the three smallest leaves on each plant indicated that on the Wisconsin plants leaves tended to become disproportionately wide with increasing length. The subtlety of this difference is shown by the fact that 95 per cent of the leaves of the two strains fell within a range common to both.

Pigment. From the time of appearance of the hypocotyl throughout the life

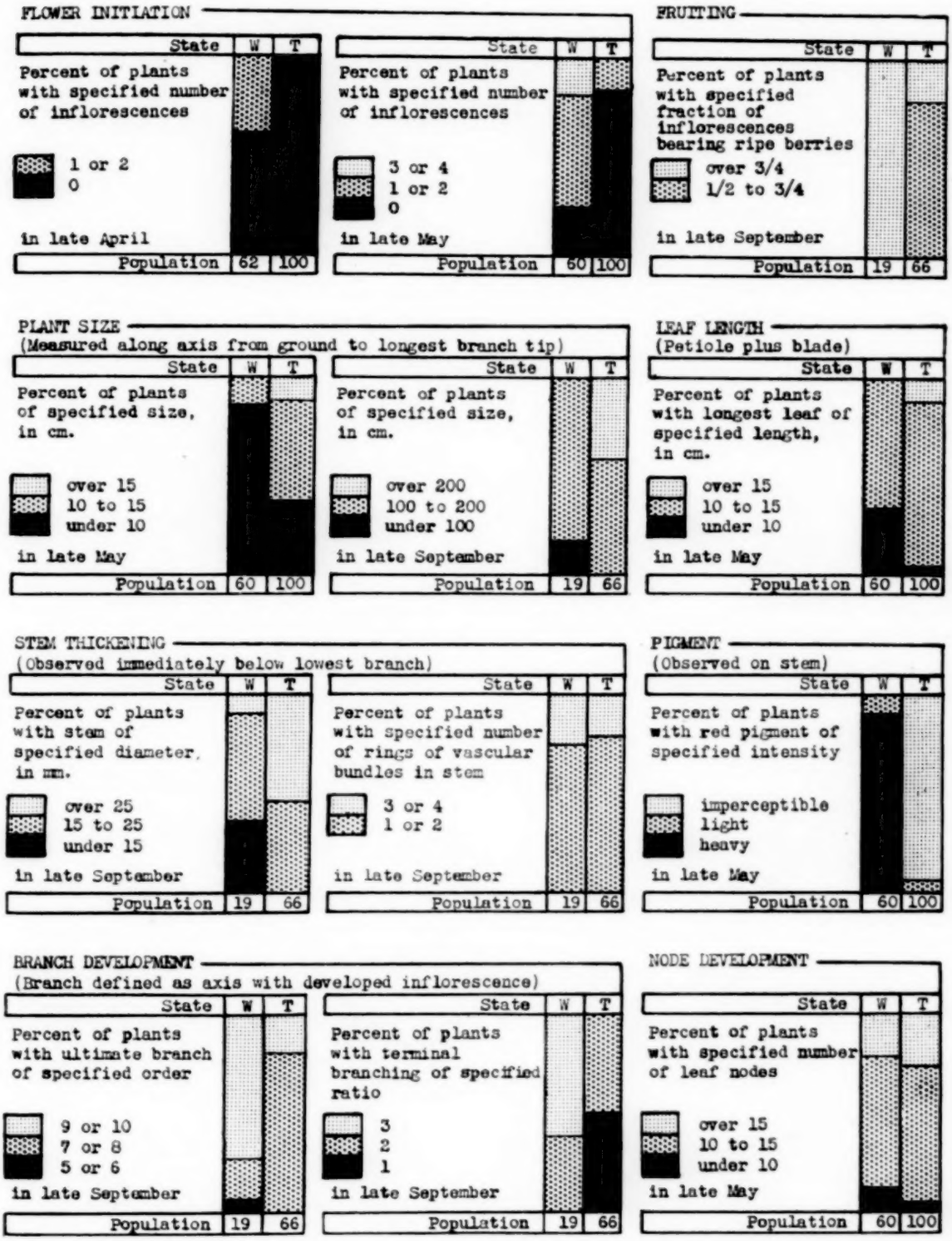

FIG. 1. Summary of contrasting characters of Wisconsin and Texas strains of poke.

of the plants, the Wisconsin strain generally had heavy red stem coloration, while few of the Texas plants developed more than a very light red pigment until late summer. Moreover the Texas plants had a brick red color quite unlike the bluish red of the Wisconsin plants. This color contrast was also conspicuous in crude extracts made from the berries. However the contrast seemed to disappear with the addition of a buffer, suggesting that it resulted merely from the familiar effect of cell sap acidity on anthocyanin color. This problem was investigated further by qualitative determinations of the absorption spectrum of the pigment by use of a Beckmann spectrophotometer. Crude extracts were obtained from berries of the two strains by boiling in water, filtering, and adding a buffer to maintain a constant pH of 3.8. There was some variation even between plants of the same strain in absorption of certain wavelengths, but all the extracts showed an identical sharp peak at about 540 mμ, as shown in figure 3. This peak corresponds to that reported for the peculiar anthocyanins found in some other

FIG. 2. Contrasting habits of Wisconsin and Texas strains of poke. (Scale is 1 meter long.)

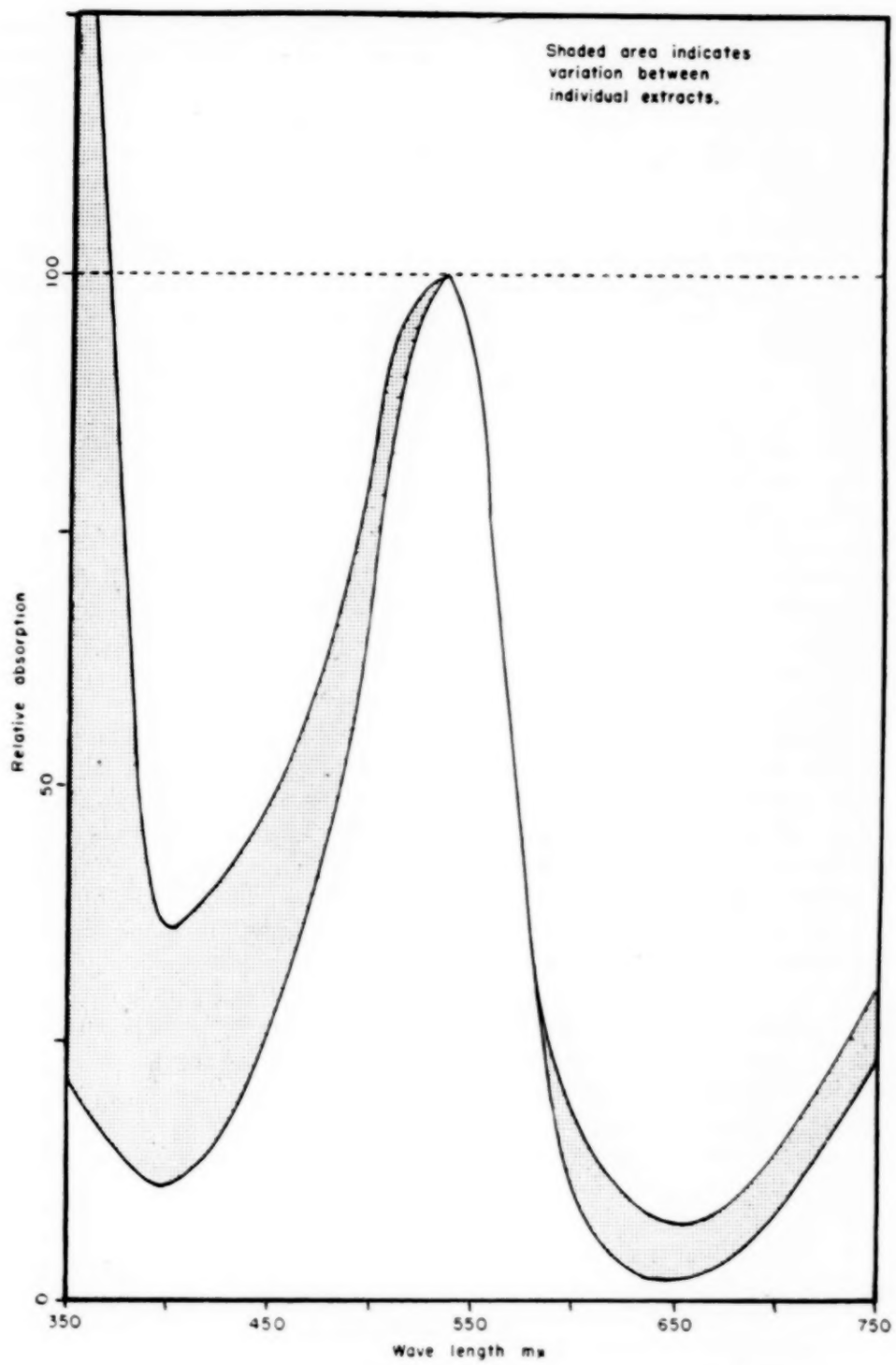

FIG. 3. Relative absorption spectra of crude extracts of pokeberries.

Centrospermae (Robinson and Robinson, 1932).

Comparison with Missouri plants. The small lot of Missouri plants grown together with the others was intermediate between the Texas and Wisconsin lots in its mortality rate, which was about 5 per cent in the greenhouse and 25 per cent in the field. In the time of flowering and fruiting, size, habit, and branching pattern, the Missouri plants were more similar to the Texas than to the Wisconsin plants. In leaf shape they were almost exactly intermediate between the other

two lots and in pigmentation they closely resembled the Wisconsin plants.

Discussion and Conclusions

This single experiment is obviously not adequate to provide a completed picture of latitudinally adapted strains of poke. Study of behavior of many strains when planted in different latitude zones would be required to fill in the picture. However an individual poke plant grows to such enormous size, for a temperate zone herb at least, that the rearing of sizable populations of the plants is not a project to be entered into lightly. Since there is no immediate prospect of a more exhaustive study, a preliminary interpretation is here attempted from the data available.

When grown under uniform conditions, strains of poke derived from near the northern and southern limits of the species range exhibited striking but not easily defined contrasts in morphology. The Wisconsin and Texas plants were so unlike in general habit that they could be distinguished at a glance from as far away as they could be seen. Measurements of various characters demonstrated apparently significant but not quite discontinuous differences between the strains.

It is remarkable that none of these differences are of a kind likely to be recognized from analysis of herbarium material. Some of the most strongly contrasting characters are not represented at all by the fragment of a poke plant which will fit on an herbarium sheet. All of the differences are quantitative and of the sort which might have been attributed to nonhereditary habitat effects in specimens not grown under uniform conditions.

Although genetic differences between the strains may be assumed to be responsible for the morphological contrasts, it is not necessary to assume that separate and specific factors are responsible for each character contrast. Most or all of the many observed differences may be simply manifestations of a basic genetically-fixed adaptation to different latitudes. Similar morphological variation is known to accompany such adaptation in other species. For example, a species of grama grass which has a latitudinal range in central North America similar to that of poke, includes a north to south series of genetically fixed strains. Olmsted (1944) has shown that quantitative morphological differences between these strains accompany the physiological differences required by adaptation to different photoperiods. In the case of poke, adaptation may be to temperature conditions rather than to day length.

Contrasts between the Wisconsin and Texas strains of poke in time of flowering and fruiting and in vigor of vegetative development are readily explainable in such terms. It is doubtful that the subtle leaf differences between the two strains are controlled by specific factors for leaf shape. On any poke plant, vigorously growing leaves tend to be narrower than old leaves; the proportionately broad leaves of the Wisconsin plants are consistent with their generally retarded growth. Contrasts in mortality and pigmentation may also be attributable to a fundamental metabolic difference, rather than to separate factors specifically controlling those characters.

In any case, the variation pattern within the single, almost isolated *Phytolacca* species of temperate North America is strikingly unlike the variation pattern in the interspecific hybrids of tropical South America which were analyzed in the preceding paper. Presumably the subtle contrasts between latitudinal strains of the North American species result from divergent evolution within a geographically continuous entity, while the clearcut, often qualitative contrasts within the South American hybrid populations result from merging of entities which had diverged during long isolation.

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NOTES AND COMMENTS

CITATION OF SPECIMENS IN CYTOTAXONOMIC LITERATURE

THEODOR JUST

Adequate citation of specimens has always been, and still is, an integral part of documentation in plant taxonomic studies. Unfortunately, the same cannot be said of many cytological contributions, especially those of earlier date. Such lack of evidence is likely to result in the eventual disregard of many earlier counts, as it will be difficult, if not impossible, to make recounts from the original slides or to examine taxonomically the plants in question. This is certainly true in regard to chromosome counts of cultivated plants (Darlington and Ammal, 1945), the infraspecific taxonomy of which is complex and often inadequately understood. Similar difficulties are bound to appear in genera of wide distribution such as *Chenopodium* (Aellen and Just, 1943), whose cytological characteristics are not well known and whose taxonomy is exceedingly involved. Other genera, even large ones, may not yield useful cytotaxonomic data at all, but show a fairly constant cytological make-up, as possibly *Eucalyptus* (Anonymous, 1950). In any case, taxonomic revision should include study of representative specimens of the populations used previously for cytological analysis. As populations are likely to change, the cytological structure of its members is equally likely to undergo changes.

Although various cytotaxonomists are keenly aware of these possibilities (see for example Cave & Constance, 1942; Godley, 1949; Jones, 1951; Manton, 1950; Rattenbury, 1948) and have themselves deposited in large herbaria specimens of plants used for cytological studies, this procedure has by no means become general practice. Consequently, it is once more recommended, as previously by other botanists (Bailey, 1949; Fosberg, 1946; Godley, 1949; Rattenbury, 1948), that representative specimens of plants used in cytotaxonomic work be deposited as vouchers in a permanent herbarium or, preferably, in several herbaria, as for instance the fine series of specimens of Hydrophyllaceae with chromosome figures distributed by Lincoln Constance, University of California. It would be both timely and desirable if an exsiccatae series of cytotaxonomic specimens could be issued following this model or similar style agreed upon by cytotaxonomists.

Another consideration pertains to the possible life span of cytological preparations (and type photographs) in comparison with that known for herbarium specimens. Barring fire, insect damage, bombing and other equally effective means of total or partial destruction, herbarium specimens last for hundreds of years. Therefore herbarium vouchers of plants used in cytological analysis are prone to outlast cytological preparations and similar documentary evidence such as photographs.

Cytologists have recently been invited to send their preparations to a common center or repository, from which these materials can be borrowed for study (Vayssière and Martens, 1949). Undoubtedly conceived with the best intentions, this project is as hazardous an undertaking as would be a central world collection of taxonomic types. In view of the irreplaceable losses of such types during World War II, wide distribution in many herbaria appears to be preferable to concentration in a single collection.

Finally, availability of cytotaxonomic vouchers in large permanent herbaria along with other specimens is bound to be an aid in bringing about a better understanding between taxonomists and cytotaxonomists.

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COMMENTS ON RECENT LITERATURE

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Hominoid Evolution and the Anatomy of the Gorilla [1]

Professor W. E. Le Gros Clark [2] recently has stated that phylogenetic problems cannot be resolved entirely by study of the anatomy of living types, and he believes that this is especially true in attempting to work out the relationships of the primates. Few modern paleoanthropologists and paleontologists will disagree with this point of view, as may be witnessed by the many important papers and monographs that have been published on the fossil primate discoveries of the past two decades. It must be admitted, however, that analysis of the usually fragmentary fossil primate remains can frequently be made more meaningful when anatomical studies of their living representatives are available.

The gorilla has been known to science for about a hundred years. During this period, many anatomists and anthropologists have considered its place among the primates and, in particular, its relationship to the hominids. These opinions have been based for the most part on the osteology and on some studies of the soft anatomy. No comprehensive anatomy of the gorilla, or for that matter of any of the other anthropoid apes, has been available, comparable to the "Anatomy of the Rhesus Monkey" by Hartman, Straus and their collaborators. This need has now been partly met by The Henry Cushier Raven Memorial Volume, "The Anatomy of the Gorilla." Arranged and edited by Professor W. K. Gregory, it includes the observations of the late H. C. Raven on the morphology of this anthropoid, together with the many excellent illustrations that were prepared under his direction. The large section on regional anatomy, to which Raven had devoted most of his attention, was completed by John Eric Hill prior to the latter's death. Other primatologists were enlisted to write the remainder of the text. S. L. Washburn prepared the part on the thoracic viscera; Herbert Elftman and William B. Atkinson, the sections on the abdominal viscera and the female reproductive system; William L. Straus, Jr., that on the microscopic anatomy of the skin; and Adolph H. Schultz, a part on morphological observations related to age changes, the dentition, the skull and certain pathological conditions.

The final result is an exceedingly useful, if not exhaustive, work on gorilla anatomy. The text is perhaps not as detailed as was originally intended by Raven, although the contributors who followed him have done an excellent job of completing the volume. It is unfortunate that circumstances prevented a fuller treatment of the skeleton and joints, or consideration of certain aspects of the soft anatomy such as the central nervous system and the organs of special sense.

All of the sections include comparisons with man and frequently with other primates. In an age when descriptive and comparative anatomy are considered by many to be passé, "The Anatomy of the Gorilla" helps to reaffirm the basic importance of accurate morphological description. Any consideration of evolutionary trends or of taxonomic relationship within the Hominoidea must have a firm morphological basis, as all workers in this group well know.

In recent years some comparative anatomists have been exploring the more dynamic aspects of their subject in an effort to evaluate adaptation and phylogenetic relationship in terms of functional as well as morphological change. This approach can do much to revitalize a field which has been practically dormant for a long time, but it requires adequate materials for comparison plus techniques that are only now in the process of being resolved. Thus far the primates have received but a small share of the attention that has been devoted to this sort of consideration. Preserved specimens of anthropoid apes are still not numerous in collections and the gorilla is the rarest of the group. In view of this, it does seem fitting that the descriptive anatomy be considered separately as a

[1] The Anatomy of the Gorilla. By Henry Cushier Raven, with contributions by W. B. Atkinson, H. Elftman, J. E. Hill, W. L. Straus, Jr., A. Schultz, and S. L. Washburn. Arranged and edited by W. K. Gregory. Columbia Univ. Press, New York. 1950.

[2] New palaeontological evidence bearing on the evolution of the Hominoidea. By W. E. Le Gros Clark. Quart. Jour. Geol. Soc. London, vol. 105, pt. 2, pp. 225–264, pls. 11–13.

fundamental contribution toward the further elucidation of the relationships of this anthropoid with the other pongids, fossil and recent, and of the Ponginae with the australopithecine primates and with the hominids.

A Review of "Diplocaulus—*A Study in Growth and Variation*" [1]

The quantitative treatment of taxonomic relationship and variability in the amphibians and reptiles has long been a puzzling problem. There is, as the author of this paper points out, "no definable terminal growth in members of these classes and no characters specifically definitive of skeletal maturity." This stands in sharp contrast to the situation in mammals where the teeth, upon eruption, have obtained a definitive size and the skeleton reaches a stage at which growth is essentially terminated.

In order to analyze growth and variation in one of the lower tetrapods, Olson selected the specialized Permian amphibian *Diplocaulus*, which has characteristic posterolateral horn-like projections on the skull appearing at a fairly early growth stage. *Diplocaulus* supposedly exhibits a high variability in skull-form that has caused much confusion in the taxonomy of this genus. The available sample consists of 47 complete and partial skulls varying in length from 14 to 147 mm. and with an adequate distribution between these limits. Some 27 measurements were made on each well-preserved skull, and as many as possible on the others.

The first part of the paper is concerned with the determination of the taxonomic relationships based on the sample. The author states that since this study ". . . was undertaken as a test case and much of the work proceeded by trial and error, the methods and results are recorded somewhat in the form of a case history of the investigation." The measurements have been coordinated into 24 "tests" or arithmetic regressions of a particular skull measurement on skull length. The estimated deviation of each specimen from the roughly plotted regression curves was determined, and this analysis indicated that only two "tests" are significant in dividing the sample into two or more groups. The frequency distribution of ratios involving orbito-snout length to skull length separated the sample into two groups. Another indication that the sample was not homogeneous was suggested by the high coefficient of variability based on these ratios (29.2), as compared with the coefficient for identical ratios in *Bufo marinus* (18.8). Frequency distributions based on several other character ratios likewise indicated separation into two groups, at least among the larger individuals.

The separation of the sample into two groups was further supported by the occurrence of the specimens in the deposits. Group A, identified as *D. magnicornis* occurs in pond, swamp and channel deposits. Group B, which is placed in the new species *D. brevirostris*, is found only in channel deposits, indicating that it lived in running water. There is reason to believe that these species bred in different environments. Although very small skulls that might be referable to *D. brevirostris* are not available, Olson believes that the two species in very small size groups could be separated on the basis of the skull length and orbito-snout relationship.

A comparison of *Diplocaulus* with certain other late Paleozoic amphibians was accomplished by utilizing four measurements that are regarded as generically stable. The purpose of this analysis was to determine if these measurements differ from the same features in genera that may be confused with *Diplocaulus*. Regressions of each measurement on skull length and ratios of skull length to each measurement were employed. Comparisons were made regardless of the size of the skulls involved. The parameters of the regressions were determined, as well as the parameters of the frequency distributions of the ratios. Comparison of the regression lines involved tests of slope and tests of coincidence of the lines. The ratios were compared through the means of their frequency distributions. The results, as might be expected, are significant for some of the comparisons, but not for others.

In order to determine the probability that single specimens assigned to other genera could belong to the sample population of *Diplocaulus*, the formula d/σ is utilized, with d equaling the absolute distance of a specimen value from the mean of the sample of *Diplocaulus* and σ the standard deviation of the sample. 3σ represents the critical level of significance. For certain characters that may be confused, the author demonstrates that the measurement ratios are often significantly different.

By making a number of length and width measurements on the skull of *Diplocaulus*, it was possible to study related changes in lateral and longitudinal growth and to evaluate these changes along the two axes. The data thus obtained provide mean values of skull dimensions at particular size levels, permitting reconstructions of mean skull outline patterns of various sizes. Both isogonic and heterogonic growth changes are noted, the latter in association with the development of the horns. Beyond the 90 mm. stage, the rapid horn growth must have been correlated with important associated functional changes presumably associated with locomotion.

The application of the coefficient of variability ($V = 100\sigma/m$) as a means of analyzing varia-

[1] By Everett C. Olson. *In*, Fieldiana: Geol., vol. 11, no. 2, pp. 57–154, 7 pls., January 12, 1951.

bility in the skulls of *D. magnicornis* is considered to be valueless. The consideration of variability in terms of V is significant only for characters or structures that have a demonstrable terminal growth. In *Diplocaulus* the differential growth rates vary in different skulls of the same lengths, producing wide diversity. The change in growth rates causes this diversity, which cannot be regarded as true variability.

The various techniques employed by Olson in this important and essentially pioneer study require much laborious computation and a suitably preserved series of specimens. The problems involved, however, have no simple solution and yet they frequently must be considered in a quantitative approach to the taxonomy and growth of fishes, amphibians and reptiles, fossil or recent. The author is to be commended for the thoroughness with which these interrelated topics have been treated.